

A MONOGRAPH ON FOSSIL BEES
(HYMENOPTERA : APOIDEA)



BY
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AND
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EDITED WITH AN APPENDIX
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By THE LATE F. E. ZEUNER AND THE LATE F. J. MANNING

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SYNOPSIS

The status of 128 species of fossil bees and nests are reviewed, 19 of which are left under open nomenclature. Four species are removed from the Apoidea. A new species *Osmia nigra* sp. nov. and subspecies *Apis* (*Synapis*) *henshawi dormiensis* subsp. nov. of bees, and two new 'species' of bees' nests *Celliforma bedfordi* sp. nov. and *Celliforma septata* sp. nov., are described. An appendix covering the years 1960-74 has been added.

I. INTRODUCTION

by S. F. Morris

UNTIL 1949, Professor Zeuner and Dr Manning had each been independently working on monographs of fossil bees, and until that time they were unaware of each other's work. But in 1949 they met and agreed to combine their efforts into a joint monograph. This collaboration continued until the death of Professor Zeuner in 1963, followed by the death of Dr Manning in 1966.

The major part of the present work was already finished by 1959, but the authors seemed to have had problems which prevented them completing it. The monograph lacks a projected part which was to have dealt with the evolution of the bees, but there are no extant manuscript notes for this. Certainly in 1964 Dr Manning was investigating a sphecoid wasp from the Jurassic of Lerida Province, Spain, which he thought might be (or be closely related to) the ancestor of the bees. No written material of this work is extant either.

Entries to the main body of the monograph ceased about 1959, so the editor has added an Appendix (p. 255) containing fossil bee references since that date, and a few earlier ones that the authors had missed which have since come to his notice. A few minor alterations to the body of the text have been made in order to bring it into line with modern taxonomic work.

Although the monograph is intended to be a world-wide catalogue of fossil bees, the authors did not have the opportunity to re-examine the American species, so that the taxonomic aspects of these are not treated in as great a depth as are the European ones. In the main the authors have had to rely on the original authors' descriptions and figures for the American species except where the specimens were deposited in a European institution.

Since this work was carried out some years ago, references to various institutions may be badly out-of-date, especially the war-damaged European museums. It has not, however, been the principle of the editor to undertake any significant alteration to the typescript as it stood. The taxonomic work as published is in two parts, the Apoidea excluding the Apidae (Section IV), and the Apidae (Section V). The division appears to have been made in this way because it most nearly represents the division between the New World and Old World fossil bees, and allows for different treatments of the two parts.

The textfigures and plates had been made but have disappeared and were not amongst the effects of either of the authors. Fortunately the British Museum (Natural History) still retained negatives of many of the photographs and these have been reprinted for the plates. No attempt has been made to redraw the missing textfigures, since it is not known what they were or what they were intended to show. New photographs have been taken of specimens that are deposited in the British Museum (Natural History).

Professor Zeuner was a Research Associate of the British Museum (Natural History), which position he had held since 1934 until his death. His obituary was published in 1963 in *Nature, Lond.* **200** : 1263. An obituary for Dr Manning appeared in 1966 in *Proc. R. ent. Soc. Lond.* (C) **31** : 62.

II. TERMINOLOGY AND CLASSIFICATION

The study of fossil bees, like that of any other group, requires a reasonably satisfactory system of classification. It may not always express fundamental relationships, but it must be consistent with the morphological evidence available. Michener (1944, 1965) attempted a revision of the families, subfamilies and tribes of bees of the world and of the North American genera in particular – a formidable task. From its very magnitude it was clear that the result would not completely satisfy the author himself, nor could it entirely agree with all the considered opinions of all bee taxonomists. His groups, however, well express relationships that have for long been obscure, and the inclusion of the bee families in the Sphecoidea has much to recommend itself. For these reasons, Michener's classification of the bees has been adopted in the present monograph.

In the past, the lack of uniformity of the use of a terminology for their morphology has been a serious difficulty in the study of bees. Fortunately Snodgrass (1935) and more recently Michener (particularly 1944) have devoted considerable time and effort to clarifying this unhappy state of affairs, and we have taken advantage of the results of the labours of these authors. Moreover, the often excellent preservation of the fossil forms makes it necessary to treat them as if they were Recent

specimens, and to make detailed reference to morphological characters. This is particularly true, for instance, of specimens from Rott which show such intimate features as wax mirrors and parts of the alimentary canal. A modern terminology, therefore, is imperative. The terms used in this monograph for the structural features of the hind legs are defined later.

With regard to wing venation the system of Ross (1936) has been adopted, together with the use of the following terms: submarginal cells, submarginal cross veins (i.e. 2nd abscissa Rs, 1st r-m, 2nd r-m) and recurrent veins (1st m-cu and 2nd m-cu). The term 'intercubitus' has become obsolete with the rejection of the use of the term 'cubital cells' for the submarginal cells. The very convenient term 'basal vein', however, is retained for the free (i.e. not fused) sections of both M and Rs, which run from opposite directions towards each other before they unite to form a vein Rs + M.

In addition, the term 'bomboid' is frequently used in the discussions that follow. This is not synonymous with '*Bombus*-like' but is intended to suggest that the characters in question are merely reminiscent of those of the tribe Bombini. Bomboid forms need not be closely related to Recent Bombini, though perhaps derived from either the ancestral form of the Bombini or, just as probably, from the ancestral form from which both the Bombini and the other Apidae arose. The last-mentioned possibility might imply that the Apini and Meliponini are not descended from the Bombini. The term 'apoid' is used in a somewhat similar sense in its appropriate context.

Other terms, important because of their evolutionary significance, are those defining certain structures of the hind legs. The most essential are the following: (1) tibial comb, (2) tibial rake, or pollen rake, (3) tibial spur, (4) auricle, (5) depstum, and (6) basitarsal brush.

The TIBIAL COMB¹ is a structure much like a comb, situated on the *outer* side of the apex of the tibia, above the tibio-basitarsal joint. It consists of strong hairs, fused at the base, which usually project backwards and downwards.

The TIBIAL RAKE is the dense row of spines or spine-like hairs along the apical edge of the *inner* side of the tibia.

The TIBIAL SPURS are the two large and sharp spines which are jointed to the tibia. They protrude from the lower apical margin of the hind tibia. In the normal walking position, with the hind legs slightly turned outwards, they have to be looked for underneath in a seemingly forward position. If two spurs are present they are distinguished as the inner and outer hind tibial spurs. The inner one is often serrate. If only one is present, it may be either the outer or the inner, and one can be distinguished from the other by its position relative to the apical rim of the tibia and by the presence or absence of serration, sometimes expanded into a comb-like structure. Thus a single spur with one edge serrate, occupying a relatively deep,

¹ The honey bee and the bumble bee lack this comb, but nevertheless have one or two hairs situated on the outer apical face of the corbicula. The derivation of these hairs is not known. Their position, however, precludes them from being direct derivatives of the tibial comb. They have not been noticed in fossil Apinae but might easily have been overlooked. They are used for stabilizing the load of pollen.

inner position, is assumed to be the inner tibial spur, and a straight spur without serration, occupying a more marginal position, is assumed to be the outer.

The AURICLE is the more or less broadened upper tip of the basitarsus which lies below the distal end of the tibia. It is like a projecting lip neatly fitting the complementary shape of the tibial apex, and in Recent *Apis* it is set with minute stud-like eminences. Often both the lip and tibial apex have been jointly termed the auricle, a practice not followed here.

DEPSTUM is a term used for an angularity of the basitarsus which is sometimes present where no true auricle is developed. This is a primitive condition, although some bees (e.g. *Meliponini*) do not even have a depstum in the modern species.

Lastly, the term BASITARSAL BRUSH is reserved for the neatly aligned rows of bristles present on the inner surface of the basitarsus of the Apini. It is not used for the haphazard arrangement of hairs found in other groups.

III. MATERIAL STUDIED

For the study of the fossil Apidae a fair amount of material was available in the British Museum (Natural History), the total number of specimens being 52. The *Meliponini*, for instance, lacked only the specimens from the Sicilian amber which had been well described and illustrated by Tosi as long ago as 1896. The Apini lacked only representatives of the bees from Randecker Maar, mainly in the Armbruster Collection, but these were examined by one of the authors. It was only in the *Bombini* that the Museum collection really lacked material, due to the extreme paucity of the fossils of this tribe. Fortunately the most important representative, *Bombus proavus* Cockerell, has been well photographed and described (1931).

Furthermore, during 1950 and again in 1951, both authors travelled independently on the European continent studying fossil Apidae. Collections in Holland, Germany and Switzerland were examined. One of us had carried on this study of continental material for a number of years before it was decided to continue the work jointly.

Whilst fossil Apoidea are plentiful in Europe, the absence of material belonging to families of bees other than the Apidae is disappointing. This material is chiefly in American museums and must await discussion by someone from there. Our attempts to obtain information or specimens from the relevant museums remained, unfortunately, without significant success. Below are given the names of the more important collections of fossil Apidae or museums where such material is to be found.

ARMBRUSTER COLLECTION. In the sediments of a small volcanic lake at Randeck, Württemberg, honey bees have been found by numerous collectors. Possibly the oldest known specimens are those in the Oscar Fraas Collection, Stuttgart. In 1926, however, William Scheuthle of Goepfingen began his search for fossil honey bees, and just over a year and a half later was assisted by Professor L. Armbruster. When the former died in November 1928, substantial discoveries had already been made and the collection eventually passed entirely into the possession of Professor

Armbruster. Other collections believed to contain Randecker Maar honey bees are those of Eduard Scheer of Goeppingen, Bernard Hauff of Holzmaden, Karl Schempf of Brucken, and Pfarrer Hermann of Holzmaden.

BAUCKHORN COLLECTION. See Siegburg an der Lahn (p. 160).

BURSEY COLLECTION. The collection of amber fossils formerly belonging to Mr Maurice Bursey of Surbiton, Surrey, now in the Muséum National d'Histoire Naturelle, Paris, contains the important specimen *E. (Electrapis) apoides* Manning (p. 227).

COCKERELL COLLECTION. The late Professor T. D. A. Cockerell of the University of Colorado collected and studied fossil bees. His main collections were made from the Miocene lake deposits of Florissant, Colorado, particularly during the expedition of 1906-7, when he was accompanied by his wife, Dr W. M. Wheeler and Mr S. A. Rohwer. His collections of fossil bees appear to have been few, and are now in the University of Colorado Museum, Boulder, Colorado, and the American Museum of Natural History. Although more of his other fossil insects are in the British Museum (Natural History), the only bee from his collection to be found there is *Anthophora melfordi* Cockerell.

DANZIG, Poland: Westpreussisches Provinzial-Museum. Many Baltic amber specimens were to be found here, but the whereabouts of the collection is not known at the present time.

KARLSRUHE i.B., Germany: Badische Landessammlung für Naturkunde, Erbprinzenstrasse 13. Contains some of the Oeningen and Radoboj material described by Oswald Heer. The building itself is in ruins, but the cellars are still packed with material and it is possible, therefore, that some further types, at present untraceable, will be found.

KLEBS COLLECTION. From time to time Baltic amber specimens were formerly sold to private collectors and to museums, and it appears that this dispersal was made by the firm of Messrs Stantien & Becker, who traded the amber and who later were taken over by the Prussian State Amber Works. Messrs Stantien & Becker, in their day, placed the amber fossils in charge of Richard Klebs (1850-1911) who was, in later years, state geologist to the Prussian Geological Survey. A set of 346 specimens, including the holotype of *E. (Roussyana) proava* Menge (p. 236), was acquired by the British Museum (Natural History) from Messrs Stantien & Becker in 1892, but since the specimens bear labels marked 'R. Klebs, Museum Stantien & Becker', this collection has usually gone under the name of 'Klebs Collection'. (See also p. 238.)

KOENIGSBERG, East Prussia, U.S.S.R.: Geologisch-Paläontologisches Institut und Museum der Universität. The most important types and described specimens of Baltic amber bees were included in this collection. They are now housed in the Museum of the Humboldt University, Berlin.

MAINZ (Rhein), Germany: Naturhistorisches Museum der Stadt Mainz. Contains a large collection of insect remains from the *Hydrobia*-limestone of the district around Mainz.

LONDON, British Museum (Natural History). See under Klebs Collection, Swinhoe, R. C. J., Luke Thomas Collection and Krantz, F. This collection includes some 52 specimens, including the types of Heyden (1862), and others from the Baltic amber, Rott am Siebengebirge, Florissant, Böttingen, East African copal, Burmese copal and South Australia.

MARSEILLE, France: Musée. According to Armbruster (1938) and Roussy (personal communication), the specimen of '*Apis*' *aquitaniensis* de Rilly (No. 5979) (p. 250) is in this collection, and Meunier (1915) states that a specimen of *Anthophorites mellona* Heer (p. 196) is also in it. No confirmation, however, can be obtained after repeated enquiries. The Marseille Museum is rich in fossil insects from the Tertiary of southern France.

ROUSSY COLLECTION. This is the private collection of Monsieur Louis Roussy, Aigle, Switzerland, and contains mainly Baltic amber specimens, including *Electrapis* (*Roussyana*) *palmnickenensis* (Roussy), p. 233.

SCHEELE COLLECTION. This important collection of several thousand specimens of Baltic amber has been purchased by the Geologisches Staatsinstitut, Hamburg. Several important specimens of *Electrapis* are included.

SIEGBURG AN DER LAHN, Germany: Städtisches Heimatmuseum. This museum contains the valuable collection of fossil insects made by Hugo Bauckhorn. It is particularly rich in specimens from Rott, previously studied by Meunier and Statz.

STATZ COLLECTION. Fossil insects from Rott am Siebengebirge have been collected for over a century and are to be found in many museums and institutions. The collection made by the late Georg Statz of Cologne has become famous for the number and quality of its specimens. Moreover, Statz described and figured large numbers of his specimens. His collection includes several dozen fossil bees some of which have been well described and play an important role in the reconstruction of the phylogeny of the group. It is much to be regretted that this collection has been removed to Algiers, where it is in the hands of the collector's daughter.

STUTTGART, Germany: Württembergische Naturaliensammlung. This collection includes the material from Boettingen Swabian Alb, a locality situated not far from Randeck. One of us, while studying the fauna of this area, discovered a fossil swarm of honey bees, and casts were made of some of the bodies comprising it. Unfortunately it is believed that the original specimens were destroyed during the war, but the casts are still preserved in the British Museum (Natural History).

SWINHOE COLLECTION. Specimens of insect inclusions in the dark and pale varieties of Burmese amber from the Hukong Valley were collected by R. C. J. Swinhoe and presented to Professor T. D. A. Cockerell. Some were later presented by Cockerell to the British Museum (Natural History). Only the pale Burmese amber is known to contain bees.

TIMON-DAVID COLLECTION, Marseille. This collection consists of fossil insects from Camoins (Bassin de Marseille) and other French localities, and includes the fossil bee *Halictus ruissatensis* Timon-David (p. 164).

LUKE THOMAS COLLECTION. A number of specimens of fossil bees are from East African copal. These, and other insects, have been presented to the British Museum (Natural History) at various times by individual donors. The Luke Thomas Collection contains twelve pieces of copal including fossil bees belonging to the Meliponini. They were presented to the British Museum (Natural History) in 1945 by Col. H. Burrows. All are from the east coast of the mainland of Africa, facing Zanzibar.

WASHINGTON, D.C., U.S.A.: United States National Museum; Smithsonian Institution. Contains part of the collection, mainly from Florissant, described by Professor T. D. A. Cockerell.

WICKHAM COLLECTION. The late Professor H. F. Wickham collected material from the Miocene shales of Florissant, Colorado, particularly at Wilson Ranch. This collection, which contains *Andrena percontusa* Cockerell (p. 167), is in Yale University.

ZÜRICH, Switzerland: Geologisches Institut und Museum der Eidgenössischen Technischen Hochschule. This collection includes much of the material, described by Oswald Heer, from Oeningen.

IV. SYSTEMATIC PALAEOONTOLOGY: SYNONYMIC LIST OF FOSSIL BEES (EXCLUDING APIDAE)

The following list is arranged according to Michener (1944, 1965). His phylogenetic groups and main diagnostic characters for families, relevant subfamilies and tribes have been quoted, even though it is sometimes doubtful whether they are applicable to fossil forms. Indeed, only completely inapplicable characters have been omitted.

In compiling the list a considerable number of specimens have been examined. In the case of unexamined material, no diagnoses of genera or species or systematic descriptions are given. These must await a study of the fossil material in American collections. Among such material, too, those specimens whose affinities have been stated in a definite way by earlier authors, but concerning which one might hold other views, have sometimes been accorded the benefit of the doubt, and noted under the generic name assigned by the most trustworthy author. The sections headed '*incertae sedis*' therefore do not include specimens which are believed to be of such a nature that more information about them may substantiate their present suggested status. It is reserved for those which are too poorly preserved to be classifiable, and for vague records which cannot be substantiated by specimens.

The publication containing the first valid name in accordance with the International Rules of Zoological Nomenclature has been marked with an asterisk (*).

Superfamily **APOIDEA** Ashmead 1899

Family **COLLETIDAE** Bingham 1897

DIAGNOSIS. Labrum broader than long; subantennal areas absent or at least reduced to small triangular spaces; lower sides of clypeus not bent parallel to long

axis of body ; subantennal sutures directed toward inner margins of antennal sockets ; facial foveae often present ; galeae short post-palpally and usually short pre-palpally, glossa short and often truncate or bifid, rarely round ; labial palpi short, segments similar but sometimes the first somewhat elongated and broadened ; pre-episternal sutures usually complete ; metanotum usually horizontal ; middle coxae, as seen from the outside, much shorter than the distance from their summits to posterior wing bases ; pygidial plate present or absent.

Many of the genera are also distinguished from practically all other bees in having the posterior part of vein 2nd m-cu (2nd recurrent) of each forewing arcuate towards the apex of the wing ; the basal vein is not strongly curved.

REMARKS. No fossil Colletidae have so far been found,² though *Cyrtapis*, a genus of Halictidae, is according to Cockerell (1908a) in some respects reminiscent of the Colletidae.

Family HALICTIDAE Ashmead 1899

DIAGNOSIS. Labrum broader than long, but in some females its apex is produced to form a broad, acutely pointed process ; subantennal areas absent, though there is usually a single subantennal suture directed towards inner margins of antennal sockets ; lower sides of clypeus not bent back parallel to long axis of body ; facial foveae ordinarily absent ; galeae elongated pre-palpally, not post-palpally, the pre-palpal section tapering evenly to an acute base ; labial palpi with segments similar to each other, and usually cylindrical, rarely are any of the first three elongate and flattened. Glossa acute, usually short, without flabellum ; pre-episternal sutures usually complete ; metanotum horizontal ; middle coxae with exposed parts much shorter than distance from summits to posterior wing bases ; basitibial plate usually present in females, except in parasitic genera ; pygidial plate present in females.

Basal vein usually strongly curved ; jugal lobe of posterior wings much more than half as long as anal lobe.

The most distinctive features are the long pre-palpal parts of the galeae, the usually strong arcuation or angulation of the 1st abscissa of basal vein (vein M), and the normally complete pre-episternal suture.

DISTRIBUTION. Oligocene to Recent.

REMARKS. Apart from the genus *Cyrtapis*, which has colletid affinities, only true Halictinae are known as fossils. By Oligocene times they appear to have been very modern in wing venation and probably in their general appearance also.

Subfamily HALICTINAE Ashmead 1899

DIAGNOSIS. Supraclypeal area convex and protuberant if seen in profile ; clypeus itself longer than labrum and not protuberant much beyond level of supraclypeal area ; labrum in females commonly provided with a broad, pointed apical process ;

² But see Appendix, p. 255.

antennal sockets not, or only a little, below middle of face ; pre-episternal suture conspicuous and complete ; scopa, when present, usually very extensive and found on posterior trochanters, femora, tibiae and basitarsi ; prepygidial fimbria usually divided by a longitudinal line without hairs or with only appressed hairs.

First abscissa of basal vein (vein M) strongly arcuate and first submarginal cell ordinarily longer than third when, as is usually the case, three are present.

Sometimes the glossa is elongated and variously modified ; the labial palpi are not elongated.

REMARKS. This large subfamily is only very moderately represented by fossils.

Genus *CYRTAPIS* Cockerell 1908

*1908a *Cyrtapis* Cockerell : 339.

1909b *Cyrtapis* Cockerell ; Cockerell : 80.

GENOTYPE. *Cyrtapis anomalus* Cockerell by monotypy.

REMARKS. According to Cockerell (1908a), 'the general appearance and the large stigma, marginal cell, and bent basal nervure are all as in the Halictines. The form of the second submarginal cell, with the first r.n. joining it before the middle, as well as the second r.n. with the double curve, suggest affinity with the Colletines'. *Cyrtapis* may well have retained primitive elements, but because its evolution is towards the Halictines it is better to look upon it, for the time being at least, as a representative of the latter. Special mention of the type was made by Cockerell (1909b).

Cyrtapis anomalus Cockerell 1908

*1908a *Cyrtapis anomalus* Cockerell : 339.

1909b *C. anomalus* Cockerell ; Cockerell : 80.

1931 *Cyrtapis anomalus* Cockerell ; Salt : 145.

HOLOTYPE. Cockerell Collection, whereabouts unknown.

DISTRIBUTION. Oligocene : Florissant.

REMARKS. Mouth parts not known. In the circumstances, and because vein 2nd m-cu (2nd recurrent) has a strong double bend, the species is considered to be a little anomalous.

Genus *HALICTUS* Latreille 1804

*1804 *Halictus* Latreille : 182.

1935b *Halictus* Latreille ; Richards : 170.

1938 *Prohalictus* Armbruster : 48, fig. 74 (type species : *P. schemppi* Armb.).

GENOTYPE. *Apis quadricincta* Fabricius, by subsequent designation of Richards (1935b : 170).

Halictus ruissatensis Timon-David 1944

1943 *Sphecodes* Timon-David : 256.

*1944 *Halictus ruissatensis* Timon-David : 42.

HOLOTYPE. Timon-David Collection, Marseille.

DISTRIBUTION. Oligocene : Bassin de Marseille.

REMARKS. Originally included by Timon-David (1943) in *Sphecodes*, but later (1944) placed, more correctly, in *Halictus*. We have not examined the specimen.

Halictus florissantellus Cockerell 1906

*1906 *Halictus florissantellus* Cockerell : 43.

1907 *Halictus florissantellus* Cockerell ; Handlirsch : 889.

HOLOTYPE. Mus. Comp. Zool. Harvard, No. 2010 (= Scudder Coll. No. 921).

DISTRIBUTION. Oligocene : Florissant.

REMARKS. The name '*florissantellus*' (Handlirsch 1907) is obviously a printer's error. Cockerell (1906) writes that only part of the wing venation is preserved, but 'generic reference seems safe'. Approximately 6.5 mm long.

Halictus miocenicus Cockerell 1909

*1909a *Halictus miocenicus* Cockerell : 160.

1931 *Halictus miocenicus* Cockerell ; Salt : 146.

HOLOTYPE. Cockerell Collection, whereabouts unknown.

DISTRIBUTION. Oligocene : Florissant.

REMARKS. According to Cockerell, the generic position is probably correct.

Halictus scudderiellus Cockerell 1906

*1906 *Halictus scudderiellus* Cockerell : 43.

1907 *Halictus Scudderiellus* Cockerell ; Handlirsch : 889.

HOLOTYPE. Mus. Comp. Zool. Harvard, No. 2011 (= Scudder Coll. No. 1966).

DISTRIBUTION. Oligocene : Florissant.

REMARKS. Appears to be correctly placed. This bee is smaller than *H. florissantellus*, being only 4.5 mm long.

Halictus schemppi (Armbruster 1938)

*1938 *Prohalictus schemppi* Armbruster : 48, fig. 74.

HOLOTYPE. Schempp Collection, Stuttgart-Weil.

PARATYPES. Three specimens, Armbruster Collection.

DISTRIBUTION. Miocene : Randeck.

REMARKS. Armbruster refers to one of his specimens as a true *Halictus*, stating (1938 : 48) that 'the nervulus is positioned quite normally'. There is no reason for believing the others are not conspecific.

Family ANDRENIDAE Latreille 1802

DIAGNOSIS. Labrum broader than long, subantennal areas defined by two subantennal sutures beneath each antennal socket ; anterior lateral margins of clypeus usually concave ; lower sides of clypeus bent backwards more or less parallel to long axis of body (except in many species of *Andrena*) but clypeus not strongly protuberant ; facial foveae usually present ; galeae short pre-palpally and usually so post-palpally ; labial palpi short, the segments similar or first segment elongated and flattened, very rarely first two segments elongated ; glossa short or long, acute, without a flabellum ; pre-episternal sutures absent or present below scrobal sutures ; metanotum horizontal ; middle coxae short as seen externally, far shorter than distance from summits to posterior wing bases. Basitibial and pygidial plates present in females.

Jugal lobe of posterior wing at least nearly three-quarters as long as anal lobe.

The most characteristic feature of this family is the presence of defined subantennal areas. Unfortunately, in some species they lie below the bases of the antennae, covered with hairs, and even when uncovered only weak sutures may be revealed.

DISTRIBUTION. Eocene to Recent.

REMARKS. Only the subfamilies Andreninae and Panurginae are represented among the fossils. *Andrena* was well characterized as a genus by the Eocene.

Subfamily ANDRENINAE Latreille 1802

DIAGNOSIS. Facial foveae large and usually covered with minute hairs giving a golden or reddish brown sheen in females, but in males foveae absent or virtually undefined and not clothed with minute hairs ; first flagellar segment rarely a little more than half as long as scape, usually much shorter ; maxillary palpi six-segmented ; segments of labial palpi cylindrical, similar to one another ; glossa usually short, acute ; pre-episternal sutures absent below scrobal sutures ; scopa present from coxae to basitarsi of posterior legs.

Pterostigma moderate to large in size ; marginal cell longer than distance from apex to wing tip, and with the apex itself pointed on the costal margin of the wing or very narrowly rounded.

REMARKS. Most fossil members of this subfamily belong to the important genus *Andrena*, and two have been placed in the extinct genera *Lithandrena* and *Pelandrena*.

Genus ANDRENA Fabricius 1775

*1775 *Andrena* Fabricius : 376.

1873 *Biareolina* Dours : 288 (type species : *B. neglecta* Dours).

1912 *Andrena* Fabricius ; Viereck : 613.

GENOTYPE. *Apis helvola* Linnaeus 1758, by subsequent designation of Viereck (1912 : 613).

DISTRIBUTION. Eocene to Recent.

Andrena wisleyi Salt 1931

*1931 *Andrena wisleyi* Salt : 141, fig. 1.

HOLOTYPE. Formerly in the Geol. Museum, Univ. Koenigsberg, but now in the Humboldt Museum, Berlin.

DISTRIBUTION. Eocene : Baltic amber.

REMARKS. Well figured and described.

Andrena clavula Cockerell 1906

*1906 *Andrena* (?) *clavula* Cockerell : 45.

1907 *Andrena* (?) *clavula* Cockerell ; Handlirsch : 889.

HOLOTYPE. Mus. Comp. Zool. Harvard, No. 2014 (= Scudder Coll. No. 6963).

DISTRIBUTION. Oligocene : Florissant.

REMARKS. Considered by Cockerell (1906) to be congeneric with *A. sepulta*. He remarked, however, that 'the shape of the abdomen is like that of a ♀ *Ceratina*, or possibly certain Halictines, but the venation does not agree with these'.

Andrena grandipes Cockerell 1911

*1911a *Andrena grandipes* Cockerell : 73.

1931 *Andrena grandipes* Cockerell ; Salt : 145.

1938 *Andrena grandipes* Cockerell ; Rodeck : 295.

HOLOTYPE. Univ. Colorado Mus., No. 8599 (with counterpart).

DISTRIBUTION. Oligocene : Florissant.

REMARKS. Cockerell (1911a) states 'agrees closely with modern *Andrena* in most respects, but is peculiar for the very broad hind tibia and basitarsus, the small eyes and the long slender marginal cell'.

Andrena hypolitha Cockerell 1908

*1908b *Andrena hypolitha* Cockerell : 328.

1931 *Andrena hypolitha* Cockerell ; Salt : 145.

1938 *Andrena hypolitha* Cockerell ; Rodeck : 295.

HOLOTYPE. Univ. Colorado Mus., No. 18736.

DISTRIBUTION. Oligocene : Florissant.

REMARKS. Differs from *A. sepulta* and *A. clavula* in various details of venation etc. It is not clear, however, how the abdomen differs from *A. clavula*.

Andrena lagopus Latreille 1809

- *1809 *Andrena lagopus* Latreille : 151.
 1873 *Biareolina neglecta* Dours : 288.
 1913a *Biareolina neglecta* Dours ; Cockerell : 346.
 1930 *Andrena lagopus* Latreille ; Schmiedeknecht : 942.

HOLOTYPE. Recent, whereabouts unknown.

FOSSIL SPECIMEN. Possibly in the United States National Museum.

DISTRIBUTION. Oligocene : probably Florissant. Also Recent.

REMARKS. Schmiedeknecht, in identifying his specimen with a Recent species, mentions but one character, namely that the side of the stigma on the marginal cell 'is conspicuously angulate or subdentate about the middle'.

Biareolina Dours is a synonym of *Andrena* Fabricius, but since it possesses two submarginal cells, it is sometimes accorded separate generic status, a practice not followed by Michener (1944). Moreover, the reduction of the number of submarginal cells from three to two occurs frequently within the same species, for instance in *Andrena*, *Halictus*, *Nomada* and others.

Andrena percontusa Cockerell 1914

- *1914 *Andrena percontusa* Cockerell : 640.
 1931 *Andrena percontusa* Cockerell ; Salt : 145.

HOLOTYPE. Wickham Collection, ? Peabody Museum, Yale.

DISTRIBUTION. Oligocene : Florissant.

REMARKS. Venation like *A. sepulta* and *A. clavula*, but a small species. Abdomen differs in shape from *A. clavula*. According to Cockerell (1914), the species can be distinguished from *A. grandipes* and *A. hypolitha* by the venation.

Andrena sepulta Cockerell 1906

- *1906 *Andrena sepulta* Cockerell : 44.
 1907 *Andrena sepulta* Cockerell ; Handlirsch : 889.

HOLOTYPE. Mus. Comp. Zool. Harvard, No. 2013 (= Scudder Coll. No. 14288).

DISTRIBUTION. Oligocene : Florissant.

REMARKS. Cockerell (1906) states 'the venation is not exactly like that of any modern species with which I have compared it but the differences are unimportant'.

Andrena primaeva Cockerell 1909

(Pl. 1, fig. 2)

- 1865 Drei Osmien ; Heer : 386 (*partim*).
 1876 Osmiae ; Heer : 43 (*partim*).
 1909c Three species of *Osmia* ; Cockerell : 316 (*partim*).
 *1909c *Andrena* (?) *primaeva* Cockerell : 316.
 1909c *Osmia primaeva* (Heer MS) ; Cockerell : 316.
 1931 *Andrena* (?) *primaeva* Cockerell ; Salt : 145.

HOLOTYPE. Eidgenössische Technische Hochschule, Zürich, No. SN.202, with counterpart.

DISTRIBUTION. Miocene: Oeningen.

DESCRIPTION AND REMARKS. Although Cockerell's references to *Osmia* are, on the whole, difficult to interpret, there is no doubt whatever that the specimen he described as *Osmia primaeva* was the holotype. The insect is reasonably well preserved but the head is lacking. The chitin is dark brown in colour which may have been the colour of the original insect. The abdomen is plump and subglobose, but, since it is a millimetre broader than the thorax, the junction of the two gives the impression of a distinct constriction.

The thorax has a large convex mesoscutum and apparently strong tegulae; the other features are indistinct.

The hind legs are fairly well preserved, the tibia and basitarsus being approximately equal, their combined length being 3.5 mm; the tibia is broad, apparently twice the width of the basitarsus, and both are copiously hairy; the femur is as broad as the tibia. The tibia and basitarsus of the middle leg are not preserved in a natural position, and we are inclined to consider Cockerell's basitarsus as the tibia and his tibia as the femur. Both femur and tibia are of the same width, but the tibia is slightly longer.

The wings are not preserved in their entirety owing to a crack in the rock. Fortunately, what is preserved is very distinct and includes the apical region of the fore and hind wings.

Forewing: long, well-developed pterostigma; marginal cell narrowing apically, and arising broadly from the pterostigma; three submarginal cells, the first not completely preserved, the second rhomboid, receiving the first recurrent vein slightly distad of the middle and having its proximal cross vein slightly hooked at the base, the third submarginal cell at least twice as large as the second, only half as broad on the marginal cell as its own base, and receiving the second recurrent vein in its last third.

Hindwing: radial sector and media continued to wing margin and cross-vein r-m only very slightly oblique.

Cockerell's (1909) statement that 'all things considered the reference to *Andrena* seems reasonably assured' appears a fair conclusion. The venation of the hind wing and the rather plump body precludes the specimen from being referred to *Halictus*.

MEASUREMENTS. Length of thorax and abdomen (head lacking) 7 mm; length of thorax 2.25 mm, width 3 mm; length of abdomen 4.75 mm, width 4 mm.

Andrena sp. indet. (Brischke)

1886 *Andrena* Brischke: 278.

1891 *Andrena* Brischke; Scudder: 686 (5915).

1907 *Andrena* Brischke; Handlirsch: 890.

1931 *Andrena* sp. Brischke; Salt: 144.

DISTRIBUTION. Eocene: Baltic amber.

REMARKS. Among Menge's and Helm's collections, investigated by Brischke, were apparently two specimens generically determined as *Andrena*, but not described.

Andrena sp. indet. (Motschulsky)

1856 *Andrena* Motschulsky : 28.

1931 *Andrena* sp. Motschulsky ; Salt : 144.

DISTRIBUTION. Eocene : Baltic amber.

REMARKS. Motschulsky merely records the occurrence of the genus.

Genus *LITHANDRENA* Cockerell 1906

*1906 *Lithandrena* Cockerell : 44.

1909b *Lithandrena* Cockerell ; Cockerell : 81.

GENOTYPE. *Lithandrena saxorum* Cockerell 1906 by monotypy.

REMARKS. According to Cockerell, 'a genus of Andrenidae, allied to *Andrena*. It differs from *Andrena* and *Nomia* in the second r.n. which is strongly bent in its upper part, straight but oblique below ; from *Andrena* alone it differs in the proportions of the submarginal cells ; and from *Nomia* also by the tip of the marginal cell, which is pointed, and a little away from the costae. The general appearance is that of an *Andrena*, but it cannot be referred to this or any other genus . . .'. Special mention of the type was made by Cockerell (1909b).

Lithandrena saxorum Cockerell 1906

*1906 *Lithandrena saxorum* Cockerell : 44.

1907 *Lithandrena saxorum* Cockerell ; Handlirsch : 889.

1909b *Lithandrena antiquorum* Cockerell ; Cockerell : 80.

HOLOTYPE. Mus. Comp. Zool. Harvard, No. 2012 (= Scudder Coll. No. 8219).

DISTRIBUTION. Oligocene : Florissant.

REMARKS. Length 8.6 mm. Venation of forewing fully described (Cockerell 1906). Head as wide as thorax, black ; flagellum stout ; abdomen light in colour with a broad entire dark band on each segment, legs hairy.

Genus *PELANDRENA* Cockerell 1909

*1909a *Pelandrena* Cockerell : 159.

1909b *Pelandrena* Cockerell ; Cockerell : 81.

GENOTYPE. *Pelandrena reducta* Cockerell 1909a by monotypy.

REMARKS. Allied to *Andrena* but with two submarginal cells on the anterior wing. Special mention of the type was made by Cockerell (1909b). The reason for the erection of this genus is not clear. It may be based only on the two submarginal cells, in which case its generic status is weak.

Pelandrena reducta Cockerell 1909

- *1909a *Pelandrena reducta* Cockerell : 160.
 1909b *Pelandrena reducta* Cockerell ; Cockerell : 81.
 1931 *Pelandrena reducta* Cockerell ; Salt : 146.
 1938 *Pelandrena reducta* Cockerell ; Rodeck : 298.

HOLOTYPE. Univ. Colorado Mus., No. 18741.

DISTRIBUTION. Oligocene : Florissant.

Subfamily PANURGINAE Leach 1815

DIAGNOSIS. Facial foveae, when present, much smaller than in Andreninae, not clothed with fine hairs, and frequently distinct in males as well as in females ; labial palpi frequently with first segment much elongated ; maxillary palpi usually six-segmented (reduced in some species of *Perdita*). Scopa primarily confined to posterior tibiae and basitarsi.

Pterostigma usually rather large ; marginal cell, which is normally not longer than distance from its own apex to apex of wing, mostly obliquely truncate apically but sometimes merely bent away from wing margin.

REMARKS. Only one fossil genus belongs to this subfamily.

Genus *LIBELLULAPIS* Cockerell 1906

- *1906 *Libellulapis* Cockerell : 42.
 1909b *Libellulapis* Cockerell ; Cockerell : 80.

GENOTYPE. *Libellulapis antiquorum* Cockerell 1906 by monotypy.

REMARKS. Cockerell (1913a), when discussing *Libellulapis wilmattae*, stated, 'A reconsideration of the genus leads me to place it in the Panurgidae where, by reason of certain features of the venation, it appears to stand rather near to *Panurgus*'. Eyes curiously prominent. Special mention of the type was made by Cockerell (1909b).

Libellulapis antiquorum Cockerell 1906

- *1906 *Libellulapis antiquorum* Cockerell : 42.
 1907 *Libellulapis antiquorum* Cockerell ; Handlirsch : 889.
 1909a *Libellulapis antiquorum* Cockerell ; Cockerell : 80.
 1938 *Libellulapis antiquorum* Cockerell ; Rodeck : 297.

HOLOTYPE. Mus. Comp. Zool. Harvard, No. 2009 (= Scudder Coll. No. 9061).

PARATYPE. Univ. Colorado Mus., No. 18740 (= Scudder Coll. No. 8560).

DISTRIBUTION. Oligocene : Florissant.

REMARKS. Cockerell (1906) considered this species different from *Halictoides maurus* (Cresson), *Hesperapis rhodoceratus* (Cockerell) and *Parandrena andrenoides* Cresson in points of venation, and believed that it did not agree with *Diandrena* or *Biareolina*.

Libellulapis wilmattae Cockerell 1913

- *1913a *Libellulapis wilmattae* Cockerell : 344, figs 2, 3.
 1931 *Libellulapis wilmattae* Cockerell ; Salt : 146.
 1938 *Libellulapis wilmattae* Cockerell ; Rodeck : 297.

HOLOTYPE. U.S. Nat. Mus., No. 58688. Counterpart, Univ. Colorado Mus., No. 18742.

DISTRIBUTION. Oligocene : Florissant.

REMARKS. Cockerell (1913a) states, 'Broad head and prominent eyes as in some Panurgi, pygidial plate as in *Dasyphoda*'.

Family ANDRENIDAE *incertae sedis**Andrenidae* gen. et sp. indet. (Handlirsch)

- 1907 (? Andrenidae) ; Handlirsch : 890.
 1931 Andrenidae ? sp. (Handlirsch) ; Salt : 144.

MATERIAL. Hofmuseum, Vienna.

DISTRIBUTION. Eocene : Baltic amber.

REMARKS. Hind leg with pollen. Head formation suggestive of *Halictus* or *Andrena*.

Andrenidae gen. et sp. indet. (Scudder)

- 1881 Andrenidae ; Scudder : 290.
 1883 Andrenidae ; Scudder : 280.
 1891 (Andrenidae) (several) ; Scudder : 682 (5872).
 1907 (Andrenidae) (mehrere) Scudder ; Handlirsch : 890.

DISTRIBUTION. Oligocene : Florissant.

REMARKS. Specimens appear to be poorly preserved.

Family MELITTIDAE Dumeril 1821

DIAGNOSIS. Labrum broader than long ; subantennal areas absent ; subantennal sutures directed, except sometimes at their upper ends, towards inner margins of antennal sockets ; lower sides of clypeus not, or only a little, bent backwards ; clypeus not protuberant. Facial foveae absent ; galeae short pre-palpally and usually so post-palpally ; labial palpi with segments similar to one another, cylindrical ; glossa short or long, acute ; pre-episternal and scrobal sutures usually absent, the former always absent below the latter ; metanotum horizontal or sub-horizontal ; middle coxae short as seen externally, much shorter than distance from their summits to posterior wing bases ; scopa confined to posterior tibiae and basitarsi, although trochanters and femora are hairy ; basitibial plates and pygidial plate present in female.

DISTRIBUTION. Eocene to Recent.

REMARKS. The subfamilies Ctenoplectrinae and Melittinae only are represented among the fossils.

Subfamily CTENOPLECTRINAE Cockerell 1920

DIAGNOSIS. Scrobal and upper parts of pre-episternal sutures are present, though of doubtful value for fossil forms; inner hind tibial spur much broadened basally and throughout its length provided with a comb of very many long fine teeth; posterior basitarsi of female nearly as broad as tibiae; pygidial plate of male absent, that of female narrow apically, greatly broadened basally.

Pterostigma hardly twice as long as broad; marginal cell considerably longer than distance from its apex to wing tip and bent gradually away from wing margin for nearly half length of cell; two submarginal cells; jugal lobe of posterior wing about half as long as anal lobe.

REMARKS. Among Recent forms this subfamily contains only the genus *Ctenoplectra* found from Australia and Africa to China. This genus, however, is not yet known in the fossil state. On the other hand, the subfamily is represented by two fossil genera *Ctenoplectrella* and *Glyptapis*. Moreover, Cockerell (1909d) maintained that the genera included in this subfamily are 'so remote from the modern members of that group that they at least form a distinct subfamily, Glyptapinae'. 'That group', however, refers to the Megachilidae to which *Ctenoplectra*, and hence *Ctenoplectrella* etc., was considered to belong. Therefore until the affinities of the *Ctenoplectra* group, both fossil and Recent, have been more clearly defined, it is not considered advisable to create a new subfamily.

Genus CTENOPLECTRELLA Cockerell 1909

*1909c *Ctenoplectrella* Cockerell: 314.

1909d *Ctenoplectrella* Cockerell; Cockerell: 19.

GENOTYPE. *Ctenoplectrella viridiceps* Cockerell 1909 by monotypy.

REMARKS. This genus appears to be closely related to *Glyptapis*. Both genera have *Ctenoplectra* as 'their nearest relative in the modern fauna'. *C. viridiceps* was first mentioned by Cockerell (1909c) with some characters, but its full description followed in a later paper (1909d). [See also Appendix, p. 255.]

Ctenoplectrella dentata Salt 1931

*1931 *Ctenoplectrella dentata* Salt: 139.

HOLOTYPE. Formerly in the Geological Museum, University of Koenigsberg, now in the Humboldt Museum, Berlin.

DISTRIBUTION. Eocene: Baltic amber.

REMARKS. Salt considers it possible that this specimen is the male of *Ctenoplectrella viridiceps* Cockerell and gives a good description and figures.

Ctenoplectrella viridiceps Cockerell 1909

- *1909c *Ctenoplectrella viridiceps* Cockerell : 314.
 1909d *Ctenoplectrella viridiceps* Cockerell ; Cockerell : 19, fig. 14.
 1931 *Ctenoplectrella viridiceps* Cockerell ; Salt : 145.

HOLOTYPE. Formerly in the Geological Museum, University of Königsberg, now in the Humboldt Museum, Berlin.

DISTRIBUTION. Eocene : Baltic amber.

REMARKS. Female, see above. This species was a small, black, stout bee, like *Glyptapis*, hardly 5 mm long. 'The eyes were bare and the sting visible'. Full description given by Cockerell (1909d).

Genus *GLYPTAPIS* Cockerell 1909

- *1909c *Glyptapis* Cockerell : 314.
 1909d *Glyptapis* Cockerell ; Cockerell : 13.

GENOTYPE. *Glyptapis mirabilis* Cockerell, by original designation.

REMARKS. This genus, together with *Ctenoplectrella*, is referred by Cockerell 'to a group from which the Megachiloids sprang'. The genus was mentioned (1909c) in connection with *G. mirabilis*, but it was not described until later (1909d).

Glyptapis fuscula Cockerell 1909

- *1909d *Glyptapis fuscula* Cockerell : 17, fig. 12.
 1931 *Glyptapis fuscula* Cockerell ; Salt : 145.

HOLOTYPE. Formerly in the Geological Museum, University of Königsberg, now in the Humboldt Museum, Berlin.

DISTRIBUTION. Eocene : Baltic amber.

REMARKS. Cockerell (1909d) mentions that the ventral side of the abdomen is clearly seen to be furnished with strong bristles, the beginning of a ventral scopa. As distinctive characters of the species he gives the very dark wings and the large stigma.

Glyptapis mirabilis Cockerell 1909

- *1909c *Glyptapis mirabilis* Cockerell : 314.
 1909d *Glyptapis mirabilis* Cockerell ; Cockerell : 14, figs 9, 10.
 1931 *Glyptapis mirabilis* Cockerell ; Salt : 146.

HOLOTYPE. Formerly in the Geological Museum, University of Königsberg, now in the Humboldt Museum, Berlin.

DISTRIBUTION. Eocene : Baltic amber.

REMARKS. The genotype, selected by Cockerell (1909d), is actually the monotype, since the genus and species were first mentioned (1909c) together, with a few

descriptive words. The specific characters are the dark brown stigma and veins, the length of the marginal cell (over 1.2 mm), the entirely black body and the punctate mesothorax.

***Glyptapis neglecta* Salt 1931**

*1931 *Glyptapis neglecta* Salt : 136, fig. 1.

HOLOTYPE. Formerly in the Geological Museum, University of Koenigsberg, now in the Humboldt Museum, Berlin.

DISTRIBUTION. Eocene : Baltic amber.

REMARKS. Well described and figured by Salt. This is the largest known *Glyptapis* from the Baltic amber.

***Glyptapis reducta* Cockerell 1909**

*1909d *Glyptapis reducta* Cockerell : 18, fig. 13.

1931 *Glyptapis reducta* Cockerell ; Salt : 146.

HOLOTYPE. Formerly in the Geological Museum, University of Koenigsberg, now in the Humboldt Museum, Berlin.

DISTRIBUTION. Eocene : Baltic amber.

REMARKS. Wings hyaline. Cockerell (1909d) regards the ferruginous stigma and veins and the length of the marginal cell (0.935 mm) as diagnostic.

***Glyptapis reticulata* Cockerell 1909**

*1909d *Glyptapis reticulata* Cockerell : 16, fig. 11.

1931 *Glyptapis reticulata* Cockerell ; Salt : 146.

1969 *Glyptapis reticula* Cockerell ; Kellner-Pillault : 521.

HOLOTYPE. Formerly in the Geological Museum, University of Koenigsberg, now in the Humboldt Museum, Berlin.

DISTRIBUTION. Eocene : Baltic amber.

REMARKS. Differs from *G. mirabilis* chiefly in the metallic crimson tints on the abdomen and the reticulate mesothorax.

Subfamily **MELITTINAE** Dumeril 1821

DIAGNOSIS. Inner hind tibial spur unmodified ; posterior basitarsi more slender than tibiae (except in male *Haplomelitta*) and shorter than tibiae ; distitarsi unusually large.

Pterostigma slender, more than twice as long as broad, its margins basad of vein are very rarely converging basally ; marginal cell longer than distance from its own apex to wing tip, the apex itself very narrowly rounded on wing margin and bent away from the latter, if at all, only apically ; three submarginal cells, second much

the smallest, the first being the largest ; jugal lobe of posterior wing nearly half as long as anal lobe (rarely three-quarters).

The species of this subfamily are of moderate size, and black. The abdomen is provided with pale pubescent fasciae, giving the appearance of certain species of *Halictus* and *Andrena*.

REMARKS. This subfamily is represented, among fossils, only by the genus *Melitta*.

Genus *MELITTA* Kirby 1802

*1802 *Melitta* Kirby : 130-134.

1935b *Melitta* Kirby ; Richards : 172.

GENOTYPE. *Melitta tricincta* Kirby 1802, selected by Richards (1935 : 172).

Melitta willardi Cockerell 1909

*1909e *Melitta willardi* Cockerell : 393.

1931 *Melitta willardi* Cockerell ; Salt : 146.

1938 *Melitta willardi* Cockerell ; Rodeck : 297.

HOLOTYPE. Univ. Colorado Mus., No. 18737.

DISTRIBUTION. Oligocene : Florissant.

REMARKS. Cockerell (1909e) writes, 'Venation normal for *Melitta*, except that the upper segment of the basal nervure is shorter'; also 'the reference of this insect to *Melitta* seems safe'.

Family *MELITTIDAE incertae sedis*

Dasyпода (s.l.) sp. indet. (Menge)

1856 *Dasyпода* Menge : 26.

1891 *Dasyпода* (vic.) Menge ; Scudder : 696 (6005).

1907 *Dasyпода* (vic.) Menge ; Handlirsch : 890.

1931 *Dasyпода* vic. Menge ; Salt : 144.

MATERIAL. Whereabouts unknown.

DISTRIBUTION. Eocene : Baltic amber.

REMARKS. An 'Andrenida, Grabwespen' was reported (Menge 1856) to resemble *Dasyпода* but 'was distinguished from it by the hind basitarsus having a blunt lateral process in front of the joint with the second tarsal segment, and the hind leg being longer than the abdomen' (transl.). The mandibles had a broad tip with three teeth and the lancet-shaped tongue had labial palps protruding. Two specimens existed, one clearly visible, the other covered with 'schimmel'.

Family *MEGACHILIDAE* Latreille 1802

DIAGNOSIS. Labrum longer than broad, widened basally to form a long line of articulation with clypeus ; subantennal areas absent ; subantennal sutures directed

towards outer margins of antennal sockets ; lower sides of clypeus not bent backwards parallel to long axis of body ; facial foveae absent ; first flagellar segment much shorter than scape ; galeae short pre-palpally, long post-palpally ; labial palpi with first two segments elongated and flattened, sheath-like, first segment usually shorter than second ; glossa linear, possessing a flabellum, pre-episternal and scrobal sutures considerably reduced or absent ; metanotum usually vertical, sometimes horizontal ; middle coxae elongate, at least half, and usually more than half, as long as distance from summits to hindwing bases ; basitibial plates absent ; scopa, when present, confined to abdominal sterna ; pygidial plate absent, except in *Lithurge*.

Pterostigma small ; submarginal cells two, the second as long, or nearly as long, as the first ; marginal cell pointed or narrowly rounded at apex, which is usually a little bent away from costal margin of wing and nearer to wing tip than to base of cell.

The most distinguishing characters are the position of the scopa, the form of the labrum and the direction taken by the subantennal sutures.

DISTRIBUTION. Eocene to Recent.

REMARKS. The subfamilies Lithurginae and Megachilinae are known as fossils, the latter being well represented in the Oligocene.

Subfamily LITHURGINAE Newman 1834

DIAGNOSIS. Face of female elevated below antennal sockets ; epistomal suture in most part absent ; mandibles in both sexes short and robust, tridentate, the middle tooth longer and more elevated than the others ; metanotum about one-eighth as long as scutellum ; coarse spiculae of tibiae arranged in two longitudinal rows on fore and middle legs, scattered on posterior legs ; posterior basitarsi slender, parallel-sided, about as long as posterior tibiae ; second abdominal tergum unusually small, posterior margin broadly rounded ; terga two to seven of male exposed and unmodified ; male with pygidial plate, female with slender remnant thereof in the form of large spine, flattened dorsally.

Jugal lobe of posterior wing about three-quarters as long as anal lobe.

REMARKS. Only one genus, *Lithurge*, is known to which both Recent and fossil forms belong.

Genus LITHURGE Latreille 1825

*1825 *Lithurge* Latreille : 463.

1827 *Lithurgus* Berthold : 467.

GENOTYPE. *Centris cornuta* Fabricius 1787 by monotypy.

Lithurge adamitica (Heer 1865)

*1865 *Apis adamitica* Heer : 386, fig. 287.

1867 *Apis adamitica* Heer ; Heer : 4, pl. 3, fig. 11.

- 1872 *Apis adamitica* Heer ; Heer : 473, fig. 287.
 1876 *Apis adamitica* Heer ; Heer : 43, fig. 287.
 1879 *Apis adamitica* Heer ; Heer : 412, fig. 329.
 1891 *Apis adamitica* Heer ; Scudder : 688 (5936).
 1907 *Apis adamitica* Heer ; Handlirsch : 892.
 1909c *Lithurgus adamicus* (Heer) ; Cockerell : 313.
 1915 *Apis adamitica* Heer ; v. Buttel-Reepen : 9, fig. 1.
 1928 *Apis adamitica* Heer ; Wheeler : 97.
 1928 *Lithurgus* Berthold ; Wheeler : 97.
 1931 *Apis adamitica* Heer ; Statz : 45.
 1938 '*Apis adamitica*' (Heer) ; Armbruster : 86.

HOLOTYPE. Eidgenössische Technische Hochschule, Zürich, V.S.4.

OTHER SPECIMENS. (1) Eidgenössische Technische Hochschule, Zürich, SN.200 ;
 (2) Badische Landessammlung für Naturkunde, Karlsruhe, Inv.1216 (Oe.95).

DISTRIBUTION. Miocene : Oeningen.

DESCRIPTION AND REMARKS. Cockerell (1909c) considered this species to be somewhat more primitive than recent *Lithurge*, possibly a near subgenus. According to him it is separated from *Apis* by its possession of only two submarginal cells. Unfortunately the holotype, which we have studied, is not well preserved and we have not succeeded in recognizing the submarginal cells. Armbruster (1938) who contributed some original remarks on it did not consider it to belong to *Apis*.

The holotype, indeed, is a somewhat elongated insect with a slender and pointed abdomen. The outlines of the wings are preserved but the venation is mostly too indistinct for satisfactory recognition. It is clear, however, that the species does not belong to the genus *Apis*, and also that the preservation of the specimen appears to have deteriorated since it was examined by Cockerell.

The following points are presented as still being of interest. The head and thorax have preserved no recognizable diagnostic characters ; the colour of the body has darkened from Cockerell's 'warm, red-brown' ; the abdomen, as Cockerell stated, is 'truncate basally, pointed apically' and, since basal intersegmental membranes are evident, may be somewhat distended ; legs are lacking ; wings are small in comparison with size of insect, and wing venation shows only the following points. Strong costal vein ; straight and short basal vein, the anterior section of which is longest ; short, stubby, pointed marginal cell ; poorly developed pterostigma. The apex of the wing, marginal cells and recurrent nerves are no longer clearly evident ; the cross vein cu-a, however, can be detected slightly distal of the juncture of basal vein on cu. While these characters obviously do not give sufficient grounds for placing the specimen generically, we must recognize that Cockerell saw it while in a better state of preservation and accept his decision in this matter.

A second specimen (Zürich, SN.200) has been studied and tentatively assigned to this species. Its head, thorax and abdomen (except the tip) are quite well preserved, but the wings are present only in traces and the legs are missing. A strong costal vein is present, and a marginal cell similar to *Lithurge*.

A third specimen (Karlsruhe, Inv.1216 (Oe.95)) may also belong here. Abdomen and thorax alone are preserved. The former, however, is well segmented and pointed, and is very reminiscent of the holotype, from which it differs only slightly

in size, i.e. length of abdomen 10 mm, as compared with 8.5 mm for the holotype. The width of the abdomen is 4.25 mm and the overall length, as preserved, i.e. without head, is 13 mm.

Finally, it is interesting to note that Heer's figure (1865 : fig. 287) differs in wing venation from his pl. 3, fig. 11 (1867), although both are presumably meant to represent the same specimen.

Subfamily **MEGACHILINAE** Latreille 1802

DIAGNOSIS. Face of female very rarely elevated below antennal sockets ; epistomal suture complete ; mandibles variously toothed, apical tooth longest, preapical tooth not elevated ; tibiae not spiculate ; posterior basitarsi much shorter than tibiae ; second abdominal tergum large, with the posterior margin usually straight, so that base of abdomen lacks the compressed aspect of *Lithurge* ; abdomen of male with fewer unmodified sterna than in *Lithurge* ; pygidial area entirely absent.

Jugal lobe of posterior wings less than half as long as anal lobe.

REMARKS. Two tribes, Anthidiini and Megachilini, are distinguished within this subfamily, both known as fossils.

Tribe **ANTHIDIINI** Michener 1944

DIAGNOSIS. Posterior margin of scutellum usually vertical or even overhanging, at a distinct angle to the dorsal surface ; integumental maculation, at least in part, pale ; claws of female cleft or at least with an inner tooth.

Inner margin of pterostigma from its base to the base of medial vein little, if at all, longer than width of pterostigma.

REMARKS. Two Recent genera are represented by fossils, and there is one extinct genus. [See also Appendix, p. 256.]

Genus **ANTHIDIUM** Fabricius 1805

*1805 *Anthidium* Fabricius : 364.

1810 *Anthidium* Fabricius ; Latreille : 439.

GENOTYPE. *Apis manicata* Linnaeus 1758, selected by Latreille (1810 : 439).

Anthidium mortuum (Meunier 1920)

*1920 *Eucera mortua* Meunier : 731, pl. 1, fig. 5, text-fig. 4.

1931 *Eucera mortua* Meunier ; Salt : 145.

1936 *Anthidium mortuum* (Meunier) ; Statz : 260, 285, 293, 294, pl. 13, fig. 38.

HOLOTYPE. Heimatmuseum Siegburg (Lahn), Bauckhorn Collection.

DISTRIBUTION. Oligocene : Rott am Siebengebirge.

REMARKS. This specimen was first described as *Eucera* by Meunier (1920). Statz (1936), on re-examining the specimen, placed it in *Anthidium*. He insisted that the venation of the fossil form was identical with that of *Anthidium*, except for

the 'nervulus' which is 'interstitial' in the fossil and 'postfurcal' in the Recent species. Since Statz was the more reliable worker of the two, we are placing this form in *Anthidium*. The possibility of a *Eucera* occurring in Rott should not, however, be wholly disregarded, since Statz is anxious to reinforce his identification by the ecological argument that *Anthidium* builds its nest in stalks and twigs, which agrees better with the Rott biotope than the steppe habitat of *Eucera*. Statz' (1936 : 260), however, states that Recent species of *Eucera* have the second recurrent vein meeting the second submarginal cell, whereas in Meunier's *Eucera mortua* it ends distad to the second submarginal cross vein as in the genus *Anthidium*.

It is also necessary to point out that Statz' discussion of this form is misleading. He describes it (1936 : 285) under the heading of 'new discoveries', whilst his figure proves it to be Meunier's holotype. Three further disconnected paragraphs appear (1936 : 260, 293, 294) in which no mention is made of the fact that he had no new specimen. The identity with Meunier's holotype is proved not only by the general shape of the fossil, but also by the frayed margin of the right forewing.

Anthidium exhumatum Cockerell 1906

*1906 *Anthidium exhumatum* Cockerell : 38.

1907 *Anthidium exhumatum* Cockerell ; Handlirsch : 888.

HOLOTYPE. Mus. Comp. Zool. Harvard, No. 2003 (= Scudder Coll. No. 13709, with counterpart, No. 11388).

PARATYPE. Scudder Coll. No. 8444.

DISTRIBUTION. Oligocene : Florissant.

REMARKS. According to Cockerell, 'not so typical an *Anthidium* as *A. scudderi*'. The paratype agrees with the holotype in the width of the marginal cell and the shape of the second discoidal. It differs in the strongly banded abdomen. He concludes, 'It appears to be a female and I have little doubt that it represents that sex in *A. exhumatum*'.

Anthidium scudderi Cockerell 1906

*1906 *Anthidium scudderi* Cockerell : 38.

1907 *Anthidium scudderi* Cockerell ; Handlirsch : 888.

HOLOTYPE. Mus. Comp. Zool. Harvard, No. 2002 (= Scudder Coll. No. 11381).

DISTRIBUTION. Oligocene : Florissant.

REMARKS. Apparently a typical *Anthidium* which can be clearly separated from *Megachile* on points of wing venation.

Genus *DIANTHIDIUM* Cockerell 1900

*1900 *Dianthidium* Cockerell : 412.

GENOTYPE. *Anthidium curvatum* Cockerell (*nec* Smith) - *Dianthidium sayi* Cockerell, by original designation (1900).

Dianthidium tertiarium Cockerell 1906*1906 *Dianthidium tertiarium* Cockerell : 39.1907 *Dianthidium tertiarium* Cockerell ; Handlirsch : 888.

HOLOTYPE. Mus. Comp. Zool. Harvard, No. 2004 (= Scudder Coll. No. 806).

DISTRIBUTION. Oligocene : Florissant.

REMARKS. This average-sized (8 mm) dark brown bee can be assumed to be correctly placed by Cockerell, in view of his intimate knowledge of the genus.

Genus **LITHANTHIDIUM** Cockerell 1911*1911b *Lithanthidium* Cockerell : 225.GENOTYPE. *Lithanthidium pertriste* Cockerell 1911 by monotypy.***Lithanthidium pertriste*** Cockerell 1911*1911b *Lithanthidium pertriste* Cockerell : 225.1931 *Lithanthidium pertriste* Cockerell ; Salt : 146.1938 *Lithanthidium pertriste* Cockerell ; Rodeck : 297.

HOLOTYPE. Univ. Colorado Mus., No. 18738.

DISTRIBUTION. Oligocene : Florissant.

REMARKS. Only a single specimen known.

Tribe **MEGACHILINI** Latreille 1802

DIAGNOSIS. Claws of female simple ; no obtrusive pale integumental maculation ; abdominal pattern often present, resulting from bands of pale hairs ; posterior part of scutellum, except in some parasitic forms, not separated by a sharp angle from dorsal surface.

Inner margin of pterostigma from its own base to base of radial vein much longer than width of pterostigma.

REMARKS. The Recent genera *Heriades*, *Megachile* and *Osmia* are represented by fossils.

Genus **HERIADES** Spinola 1808*1808 *Heriades* Spinola : 7.1810 *Heriades* Spinola ; Latreille : 439.GENOTYPE. *Apis truncorum* Linnaeus 1758, selected by Latreille (1810 : 439).

REMARKS. According to Spinola's usage, the name *Heriades* is feminine. The masculine ending, however, is used here in conformity with modern usage.

Heriades bowditchi Cockerell 1906

- *1906 *Heriades bowditchi* Cockerell : 41.
 1907 *Heriades bowditchi* Cockerell ; Handlirsch : 889.
 1938 *Heriades bowditchi* Cockerell ; Rodeck : 296.

HOLOTYPE. Mus. Comp. Zool. Harvard, No. 2007 (= Scudder Coll. No. 13761).

PARATYPE. Univ. Colorado Mus., No. 18739 (= Scudder Coll. No. 13436).

DISTRIBUTION. Oligocene : Florissant.

REMARKS. Differs from *H. laminarum* in the pronouncedly larger head and the banded abdomen.

Heriades halictinus Cockerell 1906

- *1906 *Heriades halictinus* Cockerell : 40.
 1907 *Heriades halictinus* Cockerell ; Handlirsch : 889.

HOLOTYPE. Mus. Comp. Zool. Harvard, No. 2006 (= Scudder Coll. No. 10564).

DISTRIBUTION. Oligocene : Florissant.

REMARKS. Resembles a small *Halictus* in superficial aspect, but its true affinity is indicated by wing venation. Differs from *H. laminarum* in its darker abdomen and smaller size.

Heriades laminarum Cockerell 1906

- *1906 *Heriades laminarum* Cockerell : 40.
 1907 *Heriades laminarum* Cockerell ; Handlirsch : 888.

HOLOTYPE. Mus. Comp. Zool. Harvard, No. 2005 (= Scudder Coll. No. 3062).

DISTRIBUTION. Oligocene : Florissant.

REMARKS. Cockerell maintains 'it appears to be allied to the ordinary species of *Heriades*'.

Heriades mersatus Cockerell 1923

- *1923 *Heriades mersatus* Cockerell : 371.
 1931 *Heriades mersatus* Cockerell ; Salt : 146.

HOLOTYPE. Supposedly in Colorado Museum of Natural History, but not referred to by Rodeck (1938).

DISTRIBUTION. Oligocene : Florissant.

REMARKS. Nearest to *H. halictinus*. Author 'sure' of genus.

Heriades mildredae Cockerell 1925

- *1925a *Heriades mildredae* Cockerell : 420.
 1931 *Heriades mildredae* Cockerell ; Salt : 146.
 1938 *Heriades mildredae* Cockerell ; Rodeck : 296.

HOLOTYPE. Univ. of Colorado Mus., No. 15075, with counterpart.

DISTRIBUTION. Oligocene : Florissant.

REMARKS. Cockerell remarks that this species differs conspicuously from all other *Heriades*.

***Heriades priscus* Cockerell 1917**

*1917 *Heriades priscus* Cockerell : 383.

1931 *Heriades priscus* Cockerell ; Salt : 146.

HOLOTYPE. U.S. Nat. Mus., No. 62543.

DISTRIBUTION. Oligocene : Florissant.

REMARKS. The largest *Heriades* from Florissant. A robust, hairy, black insect. Cockerell did not appear to have much doubt about its generic position.

***Heriades saxosus* Cockerell 1913**

*1913b *Heriades saxosus* Cockerell : 233.

1931 *Heriades saxosus* Cockerell ; Salt : 146.

1938 *Heriades saxosus* Cockerell ; Rodeck : 296.

HOLOTYPE. Univ. of Colorado Mus., No. 18638.

DISTRIBUTION. Oligocene : Florissant.

REMARKS. Nearest to *H. laminarum* Cockerell.

Genus **MEGACHILE** Latreille 1802

*1802a *Megachile* Latreille : 434.

1810 *Megachile* Latreille ; Latreille : 439.

1828 *Megachile* Latreille ; Curtis : pl. 218.

1841 *Chalicodoma* Lepeletier : 309.

GENOTYPE. *Apis centuncularis* Linnaeus 1758, selected by Curtis (1828).

REMARKS. The International Commission on Zoological Nomenclature recommended that the type-fixation (i.e. *Apis muraria* Retzius 1783) of Latreille be set aside and that of Curtis (1828) upheld (ICZN Opinion 219, 1954).

***Megachile amaguensis* Cockerell 1925**

*1925b *Megachile amaguensis* Cockerell : 7, pl. 1, fig. 1.

1931 *Megachile amaguensis* Cockerell ; Salt : 146.

HOLOTYPE. U.S. Nat. Mus., No. 69601.

DISTRIBUTION. Tertiary : Kudia River, Siberia.

REMARKS. Cockerell states, 'The distance of the first recurrent nervure from the base of the second submarginal cell is an unusual feature, which I do not observe in living species'.

Megachile praedicta Cockerell 1908

- *1908c *Megachile praedicta* Cockerell : 31.
 1931 *Megachile praedicta* Cockerell ; Salt : 146.

HOLOTYPE. Cockerell Collection, whereabouts unknown.

DISTRIBUTION. Oligocene : Florissant.

REMARKS. Genus confirmed by leaves cut through as though by *Megachile*.

Megachile sp. indet. (Brischke)

- 1886 *Chalicodoma* Brischke : 278.
 1891 *Chalicodoma* Brischke ; Scudder : 694 (5985).
 1907 *Chalicodoma* Brischke ; Handlirsch : 888.
 1931 *Chalicodoma* sp. Brischke ; Salt : 144.

DISTRIBUTION. Eocene : Baltic amber.

REMARKS. *Chalicodoma* Lepeletier = *Megachile* Latreille. An unnamed *Chalicodoma* was said by Brischke to occur in the Baltic amber, two specimens apparently being known to him.

Genus *OSMIA* Panzer 1806

- *1806 *Osmia* Panzer : 230.
 1810 *Osmia* Panzer ; Latreille : 439.

GENOTYPE. *Apis bicornis* Linnaeus 1758, = *Apis rufa* Linnaeus 1758, selected by Latreille (1810 : 439).

REMARKS. It has been found difficult to determine the identity of the species of *Osmia* known to Heer. The following notes may prove useful in clarifying this point.

In 1865 Heer mentioned 'Drei Osmien', having previously (1849) described one specimen, *Osmia antiqua*, in the Karlsruhe Collection. But quite a number of so-called *Osmia* are now in the collection at Zurich. These possess Heer's manuscript names and were actually placed by him in four groups : (1) *Osmia primaeva* ; (2) *Osmia* sp. ? *dubia* ; (3) *Osmia immortua* and (4) *Osmia kirbyana*. Which of these were the three referred to in 1865 is not known.

Cockerell (1909) studied the species *O. primaeva* (see p. 167) and referred it to *Andrena*. He did the same for *O. kirbyana* (see p. 202) and considered it, probably rightly, to be a wasp. No more '*Osmia*' examined by Heer were studied by Cockerell, except a now unidentifiable insect 9.5 mm in length.

Of the remaining two groups, those specimens labelled as *O. immortua* are unfortunately indeterminable, while of the two specimens labelled '*dubia*', one is superficially much like *immortua* and being also indeterminable it is best placed there (p. 187). The second specimen, however, is good and has been selected as the type of a new species (p. 185). However, '*dubia*', apart from being a manuscript descriptive term and not a name, is preoccupied by *Osmia dubia* (Germar). We have, therefore, named it *O. nigra*. [See also Appendix, p. 256.]

Osmia carbonum Heyden 1862

- *1862 *Osmia carbonum* Heyden : 75, pl. 10, figs 11, 12.
 1891 *Osmia carbonum* Heyden ; Scudder : 721 (6219).
 1907 '*Osmia carbonum*' Heyden ; Cockerell : 228.
 1907 *Osmia carbonum* Heyden ; Handlirsch : 889.
 1936 *Osmia carbonum* Heyden ; Statz : 260.

HOLOTYPE. British Museum (Natural History), 58779 (Heyden's 1862 fig. 11).

PARATYPE. British Museum (Natural History), 58768 (Heyden's 1862 fig. 12).

OTHER SPECIMENS. Mus. Comp. Zool. Harvard.

DISTRIBUTION. Oligocene : Rott.

REMARKS. Heyden's originals were badly figured. His fig. 11 is of an insect without visible wings, and the original of fig. 12, of which the counterpart existed, was a somewhat smaller insect which has at least the more proximal portions of the wings still preserved. Both are in the British Museum (Natural History) Collection, but were badly damaged by exposure to water during the war so that no information additional to that given by Heyden can be derived from them.

On the other hand, the specimens studied by Cockerell (1907) at Harvard were 'a very good specimen with reverse' and another apparently unnamed one which may be the counterpart of the paratype. Cockerell says, 'it is evident that they were not part of Heyden's material as they do not agree with his figures and descriptions'. This is certainly true as regards his 'good specimen with reverse', but his statement relating to wingless originals of *O. carbonum* is not quite correct as far as the paratype is concerned.³ Moreover, after mentioning the 'goodness' of the specimen with counterpart at Harvard, he later quite casually states it 'is indeterminate', a statement difficult to reconcile with others previously made. It now remains to be seen whether Cockerell's second specimen is the counterpart of Heyden's paratype. Should this prove to be the case, no change of nomenclature will be necessary. On the other hand, a significant difference will necessitate placing *O. carbonum* under the *gen. indet.* group, and a new name will be required for Cockerell's specimens.

Osmia antiqua Heer 1849

- *1849 *Osmia antiqua* Heer : 95, pl. 7, figs 2a, b.
 1856 *Osmia antiqua* Heer ; Giebel : 182.
 1865 Drei Osmien ; Heer : 386 (*partim*).
 1876 Osmiae ; Heer : 43 (*partim*).
 1891 *Osmia antiqua* Heer ; Scudder : 721 (6218).
 1907 *Osmia antiqua* Heer ; Handlirsch : 889.
 1909c '*Osmia*' Cockerell : 316.
 1938 *Osmia* Armbruster : 87.

³ We consider it quite possible that the specimens described by Cockerell (1907) are, in part, the same as those described by Heyden (1862) from the collection of Dr Krantz. The difficulty of identification almost certainly lies with Heyden's poor descriptions and illustrations. That certain irreconcilable anomalies, however, do exist is quite clear, e.g. the statement that no signs of visible wings are present in a specimen of Heyden's *Apis dormitans* whereas all Cockerell's specimens of *Apis* (from Rott) possess them. In the circumstances, we have decided either to be cautious where actual similarities suggest themselves, as in *Osmia carbonum*, or to regard the two sets of material as separate and distinct, as for *Apis dormitans*.

HOLOTYPE. Badische Landessammlung für Naturkunde, Karlsruhe (Oe.91), Inv.1272.

DISTRIBUTION. Miocene : Oeningen.

REMARKS. Cockerell (1909c) said this 'cannot apparently be referred to *Osmia* or any other genus with certainty'. He, however, never saw the type and is believed to have based his statement on Heer's (1849) entry of a specimen from the Karlsruhe Collection, and his rather poor illustration of it. Whether Heer (1865) intended this specimen to be included in his 'Drei Osmien' is not known, but it is assumed to be so.

We have now studied the type and, although not well preserved, the following characters can be discerned. Broad head with a suggestion of large compound eyes; parts of one fore and two hind legs, the latter, on the right, possessing distinguishable hairs; thorax well chitinized, probably not so broad as head; abdomen also well chitinized, some segmentation visible, quite broad; some details of wing venation can be discerned, but since hind- and forewing overlap, and parts are missing, it is only possible to state that what can be seen is not incompatible with the wing venation of *Osmia*, and certainly the character of the hind legs, segmentation of abdomen, colour, general habitus etc. do not rule out *Osmia* either.

MEASUREMENTS. Overall length, 12 mm; breadth of head, 4.5 mm (approx.); breadth of abdomen 5 mm; length of abdomen, 7 mm; length of forewing, 9 mm.

Osmia nigra sp. nov.

(Pl. 1, figs 5, 6)

HOLOTYPE. Eidgenössische Technische Hochschule, Zürich, Pl. I, 719.

PARATYPE. Same collection, Pl. I, 685.

DISTRIBUTION. Miocene : Oeningen.

DESCRIPTION AND REMARKS. The holotype (labelled *Osmia* sp.? *dubia*) is a comparatively small, black, insect, which is preserved in two parts, the abdomen being 5 mm distant from the head and thorax, but evidently belonging to it. The head is very imperfectly preserved but is as broad as the thorax. The thorax shows a well-developed mesoscutum. Parts of the middle and the two hind legs are preserved, and what is believed to be the hind tibia is triangular-shaped. The hind femur, however, is as strong and almost as broad as the tibia. Only the left forewing is preserved, but most of the venation can be discerned and it agrees well with *Osmia*: short, tapering marginal cell, broader at the base where it joins the pterostigma about the middle; pterostigma well defined but not particularly large; radial vein very strong; two subequal submarginal cells; basal vein short and relatively straight, of two almost equal segments, only slightly deflected at their junction; cross-vein cu-a coincident with that of basal vein at point of juncture with Cu, but posteriorly it arches slightly proximad. Abdomen clearly reveals intersegmental membranes in the distal parts.

The paratype is an insect very reminiscent of the holotype and can be regarded as conspecific. The thorax is well developed with a broad convex mesoscutum. A

middle and two hind legs are apparently preserved, with triangular tibiae. Some aspects of the abdomen are clearly shown. The specimen, however, is not generally well preserved but nevertheless corresponds with the holotype in all those characters that can be discerned except for a slightly lighter coloration. Since darker patches exist on various parts of the body, however, it is not known which was the more natural coloration for this species. No wings are preserved. Heer's manuscript name for this specimen was *Apis adamitica*, but it was clearly not the type of the latter species.

MEASUREMENTS. Holotype: length of abdomen, 6.5 mm; width, 4.5 mm; forewing length 5.5 mm (approx.). Paratype: length of abdomen 6 mm; length of thorax and abdomen (together) 10 mm.

Osmia sp. indet. (Menge)

- 1856 *Osmia* Menge : 26.
 1891 *Osmia* Menge ; Scudder : 721 (6217).
 1907 *Osmia* Menge ; Handlirsch : 889.
 1931 *Osmia* sp. Menge ; Salt : 144.

DISTRIBUTION. Eocene : Baltic amber.

REMARKS. Specimen referred to but neither described nor species determined.

Family MEGACHILIDAE *incertae sedis*

'*Apiaria*' *dubia* Germar 1849

- *1849 *Apiaria dubia* Germar : 66, pl. 2, fig. 8.
 1856 *Osmia dubia* Germar ; Giebel : 182.
 1891 *Apiaria dubia* Germar ; Scudder : 688 (5935).
 1891 *Osmia dubia* Giebel ; Scudder : 721 (6220).
 1907 (*Osmia*) *dubia* Germar ; Handlirsch : 889.

DISTRIBUTION. Oligocene : Orsberg bei Bonn.

REMARKS. Nothing appears to be known about this specimen. The correctness of Giebel's generic determination is very doubtful.

Megachilidae gen. et sp. indet.

MATERIAL. Eidgenössische Technische Hochschule, Zürich, Nos. Pl. I, 687 (with counterpart) ; Pl. I, 688 (with counterpart Pl. I, 689) ; X ; and Pl. I, 718.

DISTRIBUTION. Miocene : Oeningen.

DESCRIPTION AND REMARKS. Two of the specimens bear Heer's MS label '*immortua*'. The specimens appear to be bees, whose known parts are not incompatible with *Osmia* but whose real systematic position cannot be satisfactorily ascertained owing to lack of diagnostic characters. The state of preservation is as follows.

(1). Pl. I, 687 (and counterpart). A fairly well-chitinized insect with head, thorax, abdomen and portion of one antenna preserved, but with almost all traces of wings effaced. Body length 10 mm; length of abdomen 5.5 mm, width 3 mm; length of thorax 3.25 mm, width 3 mm. Apart from segments of the abdomen few morphological details can be discerned.

(2). Pl. I, 688 and counterpart Pl. I, 689. A poorly-defined specimen, no longer with visible wing venation though the outline of the wings themselves can be detected. Tegulae quite prominent. Body length 11 mm approx.; length of abdomen 5.5 mm, width 3.75 mm; length of thorax not accurately determinable, width 3.25 mm.

(3). One specimen marked 'X, Hymenoptera dub.' Body chitinized, dark brown in colour and comparatively well preserved, but legs and wings completely lacking. Two well-developed compound eyes present; thorax, though less well outlined, is featureless; abdominal segments, five in number, clearly in evidence. Body length 10.25 mm; length of abdomen 5 mm, width 3.25 mm; length of thorax 3.25 mm, width 3 mm.

(4). Pl. I, 718, bearing Heer's MS label *Osmia* sp.? (*dubia*). Head, thorax and abdomen are preserved, but legs are lacking and the wing venation is too indistinct for satisfactory recognition. Both the head and thorax are well chitinized and dark brown in colour, but the abdomen is paler. Body length (allowing for curved position) 10 mm approx.; length of abdomen 5 mm, width 3.5 mm; length of thorax 3.1 mm, width 3 mm (approx.).

Family ANTHOPHORIDAE Dahlbom 1835

DIAGNOSIS. Labrum usually broader than long, attached by rather short margin to clypeus; subantennal areas absent; subantennal sutures directed towards inner margins of antennal sockets; lower sides of clypeus frequently bent back parallel to long axis of body; facial foveae almost always absent; galeae elongate post-palpally, short pre-palpally; labial palpi with first two segments elongate and flattened, first segment at least as long as second; glossa linear, usually with a flabellum; pre-episternal suture usually absent below scrobal suture, present above it; middle coxae elongate, except in a few parasitic forms; basitibial plates usually present; scopa, when present, occurs on the posterior tibiae and basitarsi, and very rarely found on abdominal sternites as well; pygidial area often present.

Usually three submarginal cells; when two only, second often much shorter than first; rarely only one closed submarginal cell.

DISTRIBUTION. Eocene to Recent.

Subfamily XYLOCOPINAE Latreille 1802

DIAGNOSIS. Clypeus not protuberant but relatively flat, lateral portions seen from beneath a little bent backward and more nearly transverse than longitudinal; pygidial plate absent, represented in some females by a flat-topped apical spine which, unfortunately, is hidden in a dense pygidial fimbria and hence would be

difficult to see in fossils; scopa of female not forming a corbicula; inner apical margins of posterior tibiae bare or hairy, without a hind tibial rake.

Michener (1944) also mentions a further distinctive feature of the clypeus of Xylocopinae, though of doubtful use for fossils. The portions of the epistomal suture between the anterior tentorial pits and the dorsolateral angles of the clypeus are subparallel to one another, while below the pits the clypeus broadens abruptly.

REMARKS. This subfamily contains two distinctive tribes, the Ceratinini and the Xylocopini, both represented by fossil forms.

Tribe CERATININI Latreille 1802

DIAGNOSIS. Small, rather slender bees with little pubescence; mandibles very broad basally but abruptly narrowing to the slender, subparallel-sided apical portions; metanotum horizontal; apex of seventh tergum of the female produced to a small, sharp, median point.

Wing surfaces hairy throughout, not papillate; marginal cell broad, longer than distance from its own apex to wing tip, and considerably bent from the wing margin apically; jugal lobe of each hindwing is one-third to half as long as the anal lobe.

REMARKS. Only one fossil specimen so far known.

Genus CERATINA Latreille 1802

1802a *Clavicera* Latreille: 432.

*1802b *Ceratina* Latreille: 380.

GENOTYPE. (*Hylaeus albilabris* Fabricius 1793) = *Apis cucurbitina* Rossi 1792, by monotypy.

REMARKS. A recommendation is before the International Commission on Zoological Nomenclature that the name *Clavicera* be suppressed.

Ceratina disrupta Cockerell 1906

*1906 *Ceratina disrupta* Cockerell: 37.

1907 *Ceratina* Cockerell; Handlirsch: 891.

1973 *Ceratina disrupta* Cockerell; Daly: 15, pl. 2, text-fig. 4b.

HOLOTYPE. Mus. Comp. Zool. Harvard, No. 2001 (= Scudder Coll. No. 9355).

DISTRIBUTION. Oligocene: Florissant.

REMARKS. This black, average-sized bee (8 mm) has the general appearance of a *Ceratina*. Description of forewing given by Cockerell.

Tribe XYLOCOPINI Latreille 1802

DIAGNOSIS. Large, robust bees with coarse, plumose hair; metanotum vertical; apex of seventh tergum of female produced to a flat-topped spine, largely hidden in a dense mass of hair; basitarsi fully as long as the corresponding tibiae.

Wings elongate, papillate distally; marginal cell very slender, its apex bent away from the wing margin and the cell itself much longer than the distance from its own apex to the wing tip; jugal lobe of hindwing much shorter than the anal lobe.

REMARKS. All fossils have been assigned to the genus *Xylocopa*.

Genus *XYLOCOPA* Latreille 1802

1802a *Xylocopa* Latreille : 432.

*1802b *Xylocopa* Latreille : 379.

1810 *Xylocopa* Latreille; Latreille : 439.

GENOTYPE. *Apis violacea* Linnaeus 1758, selected by Latreille (1810 : 439).

REMARKS. The name *Xylocopa* has been placed on the list of *nomina conservanda* (ICZN Opinion 743).

Xylocopa friesei Statz 1936

*1936 *Xylocopa friesei* Statz : 284, 293, pl. 8, fig. 37.

HOLOTYPE. Statz Collection.

DISTRIBUTION. Oligocene : Rott.

REMARKS. Wing, thorax and hind basitarsus all strongly suggest a *Xylocopa*. According to Statz, the specimen is similar in size to *Xylocopa senilis* Heer, but since only the thorax, right forewing and four legs (two very fragmentary) are known, his statement can have but limited value.

Xylocopa hydrobiae Zeuner 1938

*1938 *Xylocopa hydrobiae* Zeuner : 127, figs 20, 21.

HOLOTYPE. Nat. Hist. Mus. Mainz, Hydrobienkalk Collection, No. 123.

PARATYPE. Same collection, No. 5.

DISTRIBUTION. Miocene : Biebrich nr Mainz.

REMARKS. Vein 2nd r-m together with distal segment of Rs is Z-shaped.

Xylocopa jurinei (Heer 1865)

*1865 *Bombus jurinei* Heer : 386, fig. 296.

1867 *Bombus jurinei* Heer; Heer : 4, pl. 3, fig. 8.

1872 *Bombus jurinei* Heer; Heer : 473, fig. 296.

1876 *Bombus jurinei* Heer; Heer : 43, fig. 296.

1879 *Bombus jurinei* Heer; Heer : 411, fig. 338.

1891 *Bombus jurinei* Heer; Scudder : 690 (5953).

1907 *Bombus jurinei* Heer; Handlirsch : 892.

1909c *Xylocopa jurinei* (Heer); Cockerell : 315.

1928 *Bombus jurinei* Heer; Wheeler : 97.

1928 *Xylocopa* Wheeler : 97.

- 1931 *Bombus jurinei* Heer ; Cockerell : 301.
 1931 *Xylocopa* Latreille ; Cockerell : 301.
 1938 *Bombus jurinei* Heer ; Armbruster : 87.

HOLOTYPE. Eidgenössische Technische Hochschule, Zürich, No. Pl. I, 682a (Heer 1865 : fig. 296).

OTHER MATERIAL. Same collection, No. Pl. I, 682b (Heer 1867 : pl. 3, fig. 8).

DISTRIBUTION. Miocene (Sarmatian) : Oeningen.

REMARKS. If the specimen No. Pl. I, 682b is not the counterpart of the holotype, a point very difficult to decide, then Cockerell (1909c) did not see the type, since his specimen was that figured by Heer (1867).

Of this specimen, Cockerell (1909c) states, 'Only part of the venation can be made out, but all that can be seen agrees with *Xylocopa*, and not with *Bombus*'. Armbruster (1938) also suggests the name *Xylocopa* for this specimen. Having examined the two existing specimens, we endorse Cockerell's conclusion as applicable to both. Moreover, the tibia and basitarsus of the hind legs bear a well-developed scopa, which is typical of *Xylocopa*. Furthermore, in specimen Pl. I, 682b, the basitarsus of the hind leg is approximately one and a half times as long as the tibia. This greater length of the basitarsus is a character of *Xylocopa*, whilst in *Bombus* the basitarsus is usually shorter than the tibia. The suture between mesoscutum and mesoscutellum is very distinct in the fossils and reminiscent of *Xylocopa*. A prominent feature of specimen Pl. I, 682b is the strong and copious hairs protruding from the apex of the abdomen, which again is observed in some *Xylocopa*.

The species is distinguished from *Xylocopa senilis* Heer by its larger size.

MEASUREMENTS. Holotype : length of thorax plus abdomen, 21 mm ; length of abdomen 14 mm, width 11 mm ; length of thorax 7 mm, width 8 mm ; length of forewing 15 mm.

Specimen Pl. I, 682b : length of thorax plus abdomen 25 mm ; length of abdomen 18 mm, width 11.5 mm ; length of thorax 7 mm, width 8 mm ; length of forewing 16.5 mm. The legs here are well preserved, the length of the tibia being 3.75 mm and the length of the basitarsus 6 mm. It will also be noticed that the measurements of the thorax and the abdomen do not quite tally with those given by Heer.

Both specimens have the head missing.

Xylocopa senilis Heer 1849

(Pl. I, figs 3, 4)

- *1849 *Xylocopa senilis* Heer : 93, pl. 7, figs 1a, b, c.
 1856 *Xylocopa senilis* Heer ; Giebel : 181.
 1865 *Xylocopa senilis* Heer ; Heer : 386, fig. 295.
 1872 *Xylocopa senilis* Heer ; Heer : 473, fig. 295.
 1876 *Xylocopa senilis* Heer ; Heer : 43, fig. 295.
 1879 *Xylocopa senilis* Heer ; Heer : 411, fig. 337.
 1885 *Xylocopa senilis* Heer ; Scudder : 819, fig. 1109.
 1887 *Xylocopa senilis* Heer ; Scudder : 821, fig. 1126.
 1891 *Xylocopa senilis* Heer ; Scudder : 734 (6334).
 1907 *Xylocopa senilis* Heer ; Handlirsch : 891.

1909c *Xylocopa senilis* Heer ; Cockerell : 415.

1931 *Xylocopa senilis* Heer ; Pongrácz : 117, pls (5) 7, (6) 8.

1938 *Xylocopa senilis* Heer ; Armbruster : 88.

HOLOTYPE. Badische Landessammlung für Naturkunde, Karlsruhe, Inv.1267.

PARATYPE. Same collection.

OTHER MATERIAL. Same collection Inv.1270 (as photographed by Pongrácz 1931 : pl. (5) 7) ; Inv.1175 (Oe.89, no. 145) ; Inv.1175 (Oe.89, no. 146) ; Inv.1228 (Oe.93). Also Eidgenössische Technische Hochschule, Zürich, no. 21A with counterpart no. 21b, and another specimen doubtfully referred here, no. 21c.

DISTRIBUTION. Miocene : Oeningen.

REMARKS. We have studied specimens Inv.1175 (no. 145), Inv.1175 (no. 146) and Inv.1228 from Karlsruhe, and specimens 21A, b and c from Zürich. It is quite clear that we have not seen the holotype in spite of the fact that we made a thorough search for it at Karlsruhe, but we believe a photograph of it was published by Pongrácz (1931c : pl. (6) 8). The strongest evidence for this is the clear reference to the well-preserved antennae. The paratype, as defined by Heer, was 'ein sehr undeutliches Stück aus derselben Sammlung'. That we have not seen this specimen is again evident. Possibly it is the second one photographed by Pongrácz (1931 : pl. (5) 7) although the outline here is quite clear, and not indistinct as Heer suggested. Both types may now be lost but this cannot by any means be asserted since much material is still stored below the ruins of what was once the Badische Landessammlung, Karlsruhe.

In the absence of types it is difficult to know whether this is a genuine *Xylocopa* or not. At least, the specimens at Karlsruhe that have been examined are known to lack decisive detail for generic determination. The following are the measurements and characters that can be more reliably ascertained.

Inv.1175 (no. 145). Overall length 20 mm ; breadth of abdomen 8 mm ; breadth of thorax 5 mm ; length of wing on left 18 mm ; length of wing on right 14 mm. The impression of this insect is distinct and possibly a single leg is displayed on the left.

Inv.1175 (no. 146). Overall length 21.25 mm ; breadth of abdomen 8 mm ; breadth of thorax 5 mm ; length of wing on left 15 mm ; that on right 17 mm. This insect resembles no. 145, though it is not the counterpart. It is less distinctly preserved.

Inv.1228. Overall length 19 mm ; length of abdomen 12 mm ; breadth of abdomen 8 mm ; breadth of thorax 6 mm. This is a large brownish-black insect in which a few proximal veins of the wing can still be discerned, but not enough to serve any useful purpose. Very few other features are preserved.

On the other hand, the Zürich Collection contains a better preserved specimen (no. 21A, b) which shows enough of the venation of the forewing to identify it as a *Xylocopa*, the basal vein being short and the '2nd discoidal' cell (i.e. 2nd M) elongate. The copious hairs on the basitarsus of what appears to be the middle leg and the shortness of the remaining tarsal segments support this identification. Since the size agrees very well with that of *Xylocopa senilis* Heer, the specimen is assigned to

this species without reservation. It is the best preserved specimen available, and has the following measurements: overall length 22 mm; length of abdomen 12 mm, width 8-9 mm; length of thorax 7 mm, width 9 mm; length of forewing 8 mm. The head is rather crushed and thus of little value for measurement since it is too much spread out. The broad thorax indicates a distinct transverse suture of the notum.

Specimen no. 21c is poorly preserved, without recognizable venation. The abdomen appears to be more slender than normal for the species. Its specific and even generic identity is open to grave doubt, though it was labelled '*Xylocopa senilis* × Hr. (?)' in Heer's time. It is a smaller insect, possibly little more than 10 mm long, with a greater constriction between thorax and abdomen.

Subfamily ANTHOPHORINAE Dahlbom 1835

DIAGNOSIS. Clypeus almost always protuberant so that lateral portions, seen from below, are bent posteriorly and lie parallel to the long axis of the body; the margins of the clypeus generally converge upward to the dorsolateral angles; pygidial plate present in nearly all females and most males; scopa of female not forming a corbicula; anterior coxae usually little broader than long; inner apical margins of posterior tibiae bare or hairy, without a tibial rake.

REMARKS. This very large subfamily is believed by Michener (1944) to be a monophyletic unit. The characters, however, of parasitic forms, which have evolved along different lines, are sometimes difficult to reconcile with those of non-parasitic forms, and are not always compatible with the diagnostic characters given above. The tribes Eucerini, Anthophorini and Melectini are represented by fossil forms. [See also Appendix, p. 256.]

Tribe EU CERINI Latreille 1802

DIAGNOSIS. Large, pollen-collecting bees; clypeus of the male usually partly yellow or white; antennae of males usually much elongated; flagellar segment in the female and in some males nearly as long as the scape; posterior legs of the male only rarely enlarged or modified; arolia present; scopa present; males often possess distinct pygidial and basitibial plates.

Wing pubescent throughout and only feebly papillate apically; marginal cell as long as, or longer than, the distance from its own apex to the wing tip, its apex narrowly rounded and bent gradually away from the wing margin; most (including all North American) genera with three submarginal cells, the first and third longer than the second; second abscissa of vein M-Cu of the posterior wings usually nearly twice as long as the transverse or somewhat oblique cu-a (comparable with Emphorini) and the jugal lobe about half as long as the anal lobe; pterostigma reduced, tapering little, if at all, beyond the base of vein r.

REMARKS. The long paraglossae in the Eucerini are of doubtful diagnostic value for fossil forms. This tribe is one of the largest of the Anthophorinae but is represented with reasonable certainty by only one fossil specimen (*Tetralonia berlandi*).

Another species, *Eucera mortua*, described by Meunier (1920) has now been placed in *Anthidium*, but it is clear that Meunier felt very sure of his genus. The specimen, therefore, should be re-examined. That this was not done by us was due to our being misled by Statz's erroneous statements (see *Anthidium mortuum* (Meunier), p. 178).

Genus *TETRALONIA* Spinola 1838

1810 *Macrocera* Latreille (*nec* Meigen) : 339.

*1838 *Tetralonia* Spinola : 538.

GENOTYPE. *Eucera antennata* Fabricius 1793 (= *Apis malvae* Rossi 1790) by subsequent designation of Sandhouse (1943 : 603).

Tetralonia berlandi Théobald 1937

*1937 *Tetralonia berlandi* Théobald : 131, pl. 2, fig. 11 ; pl. 10, fig. 1.

HOLOTYPE. Museum at Marseille, Célas Collection, no. C.31.

DISTRIBUTION. Oligocene, Sannoisien du Gard, France.

REMARKS. This broad, black bee most closely approaches to the Recent *T. dwaucelii* Lepel., according to Théobald. It is 10 mm long, with the forewing measuring 6 mm in length. The specimen is adequately described and figured, and Théobald's figure certainly suggests an anthophorid.

Tribe ANTHOPHORINI Dahlbom 1835

DIAGNOSIS. Moderate-sized to large, pollen-collecting Anthophorinae ; clypeus of male usually pale ; posterior angles of mandibles are beneath posterior margins of eyes ; first flagellar segment often elongated, sometimes as long as the scape ; scopa not large, consisting of simple, or slightly plumose, hairs, or in some cases with some plumose hairs intermixed ; claws of male cleft, of female with median tooth on inner side ; arolia mostly present ; eighth tergum of male is usually bilobed, without a pygidial plate.

Wings largely bare and strongly papillate apically ; pterostigma small, usually one and a half times as long as broad and ending at the base of vein 1 ; marginal cell slightly shorter than the distance from its own apex to the wing tip, rounded at its apex ; first submarginal cell, usually slightly longer on posterior margin than are the subequal second and third cells ; jugal lobe of posterior wing usually a little over one-third as long as anal lobe ; second abscissa of vein M-Cu of posterior wings about as long as cu-a.

REMARKS. The genera *Anthophora* and *Anthophorites* are represented by fossil forms. The latter genus was erected by Heer (1849) for all fossil bees with affinities with *Anthophora*. The type, *Anthophorites mellona* Heer, therefore, is in need of further examination to establish its true relationship.

Genus *ANTHOPHORA* Latreille 1803

1802a *Podalirius* Latreille : 430.

*1803 *Anthophora* Latreille : 167.

1810 *Anthophora* Latreille ; Latreille : 439.

GENOTYPE. *Megilla pilipes* Fabricius 1775 (= *Apis acervorum* Linnaeus 1758), selected by Latreille (1810).

REMARKS. The International Commission of Zoological Nomenclature has recommended that the generic name *Podalirius* Latreille (1802) be rejected (ICZN Opinion 151, 1944).

Anthophora melfordi Cockerell 1908

(Pl. 1, fig. 1)

*1908b *Anthophora melfordi* Cockerell : 323.

1908d *Anthophora melfordi* Cockerell ; Cockerell : 575, fig. 6.

1931 *Anthophora melfordi* Cockerell ; Salt : 145.

1938 *Anthophora melfordi* Cockerell ; Rodeck : 295.

HOLOTYPE. British Museum (Natural History), I.9259. Counterpart in Colorado University Museum, No. 18922.

DISTRIBUTION. Oligocene : Florissant.

REMARKS. According to Cockerell (1908b), 'This is the first genuine fossil *Anthophora*'. The parts preserved include the head, thorax, first abdominal segment, parts of three legs, most of the forewing overlying remnants of the hindwing and the extended mouth parts.

The specimen has been re-examined and the following points noted. The forewing is well preserved, except distally. In the hindwing, however, since it is overlain by the forewing, the venation is less readily ascertainable. Some veins appear to be very badly preserved or not at all. The legs, although undoubtedly hairy, are possibly not so to the extent Cockerell suggests, nor are we able to verify his statement of the 'copious' quantity of hair on the 'tongue'.

As regards the venation of the forewing, there is no need for us to differ from Cockerell's decision to place the specimen in *Anthophora*. The juncture, however, where the first recurrent vein reaches the second submarginal cell, may be 'near the beginning of its last third instead of at the middle', but it must also be mentioned that this juncture is far from being clearly visible. Vein cu-a of the hindwing is very oblique, as Cockerell states.

Genus *ANTHOPHORITES* Heer 1849

*1849 *Anthophorites* Heer : 97.

1909c *Anthophorites* Heer ; Cockerell : 315.

GENOTYPE. *Anthophorites mellona* Heer (1849), selected by Cockerell (1909c).

REMARKS. According to Cockerell, '*Anthophorites* cannot be precisely defined, but includes various fossil bees supposed to be more or less similar to *Anthophora*'.

The genus is obviously a repository for all Anthophorid-like insects that cannot otherwise be satisfactorily determined.

The holotype of the genotypic species is now lost, but it was illustrated by Heer with some wing venation and body characters, insufficient for the establishment of a generic diagnosis. We have, however, refrained from sinking this genus because no specimens attributable to the type species have been examined by us.

Anthophorites gaudryi Oustalet 1870

- *1870 *Anthophorites gaudryi* Oustalet : 104, pl. 2, figs 11, 13.
 1891 *Anthophorites gaudryi* Oustalet ; Scudder : 687 (5922).
 1907 *Anthophorites gaudryi* Oustalet ; Cockerell : 227.
 1907 *Anthophorites gaudryi* Oustalet ; Handlirsch : 890.
 1937 *Anthophorites gaudryi* Oustalet ; Théobald : 433.

HOLOTYPE. Museum at Corent, France.

DISTRIBUTION. Oligocene (Stampian) : Corent, France.

REMARKS. The specimen is poorly preserved and lacks the head. Scudder (1891) compared it with *A. parietaria*. Cockerell (1907) writes, 'has a curiously fly-like appearance', and 'its hairs are not plumose'. Oustalet's figure (1870 : pl. 2, fig. 11) is most difficult to interpret.

It should be noted that the species is not listed by Théobald (1937 : 375) where *A. mellona* is given as occurring at Corent instead.

Anthophorites thoracica Heer 1867

- *1867 *Anthophorites thoracica* Heer : 6, pl. 3, fig. 14.
 1891 *Anthophorites thoracicus* Heer ; Scudder : 687 (5925).
 1907 *Anthophorites thoracicus* Heer ; Handlirsch : 890.

HOLOTYPE. Possibly Badische Landessammlungen für Naturkunde, Karlsruhe.

DISTRIBUTION. Miocene : Radoboj.

REMARKS. Apparently based on one specimen from Radoboj. We particularly searched for this specimen at Karlsruhe without avail. It may nevertheless still reappear when the material now stored in the cellars there is unpacked and sorted.

Anthophorites longaeva Heer 1867

- *1867 *Anthophorites longaeva* Heer : 5, pl. 3, figs 12, 13.
 1891 *Anthophorites longaevus* Heer ; Scudder : 687 (5923).
 1907 *Anthophorites longaevus* Heer ; Handlirsch : 890.
 1909c *Anthophorites longaeva* Heer ; Cockerell : 315.
 1938 *Anthophorites longaeva* Heer ; Armbruster : 87.

HOLOTYPE. Heer's (1867) fig. 13 from Radoboj. Whereabouts unknown.

PARATYPE. Heer's (1867) fig. 12 from Oeningen. Whereabouts unknown.

OTHER SPECIMENS. Eidgenössische Technische Hochschule, Zürich, Nos Pl. I, 683, Pl. I, 712 and Pl. I, 809.

DISTRIBUTION. Lower and Upper Miocene : Radoboj and Oeningen.

REMARKS. Of the two specimens figured by Heer (1867), fig. 13, from Radoboj, appears to be well preserved. Fig. 12, from Oeningen, however, is described as 'sehr ähnlich *A. mellona*, aber beträchtlich grösser'. It is believed to have been seen by Cockerell (1909c) who described it as a bee with large eyes, narrow face, middle joints of a rather stout flagellum a little longer than broad, and an abdomen broad at the base, with fine hair ; hind tibia 3.75 mm, hind basitarsus 2.5 mm and broadened ; venation indistinguishable. The generic position of the specimen was considered by Cockerell to be 'wholly obscure'. The three Zürich specimens can be described as follows.

Pl. I, 683. A strongly chitinized insect having the head partly lacking ; thorax well outlined, but without distinct diagnostic characters ; abdomen with segments clearly indicated and covered with hairs ; hind legs poorly preserved, the basitarsus and tibia apparently hairy. Body length 16 mm ; length of abdomen 10 mm, width 5 mm ; length of thorax 4 mm, width 4 mm.

Pl. I, 712. Head, thorax and abdomen preserved, but not so highly chitinized as Pl. I, 683 ; the strong costa of the wing can be discerned ; abdomen somewhat distended ; a triangular-shaped chitinous area that is preserved may be a tibia. Length of body 17 mm ; length of head 2.25 mm ; length of thorax 4.5 mm, width 4.5 mm ; length of abdomen 10.25 mm, width 5.75 mm.

Pl. I, 809. A very weakly chitinized specimen on which few details can be discerned. Head, thorax and abdomen present, wings completely lacking and legs practically absent. Length of body 17.5 mm ; length of head 2 mm ; length of thorax 5 mm, width 5 mm ; length of abdomen 10.5 mm, width 6 mm.

These three specimens are not determinable. They are placed under this species because the characteristics that can be discerned are compatible with the holotype. They are labelled with the name *A. longaeva* in a nineteenth-century handwriting.

Anthophorites mellona Heer 1849

- *1849 *Anthophorites mellona* Heer : 97, pl. 7, figs 4a-c.
- 1856 *Anthophorites mellona* Heer ; Giebel : 183.
- 1891 *Anthophorites mellona* Heer ; Scudder : 687 (5924).
- 1907 *Anthophorites mellona* Heer ; Handlirsch : 891.
- 1907 *Anthophorites mellona* Heer ; Cockerell : 229.
- 1909c *Anthophorites mellona* Heer ; Cockerell : 315.
- 1914 *Anthophorites mellona* Heer ; Meunier : 193, pl. 6, figs 5a, b, text-fig. 5.
- 1937 *Anthophorites melona* (Heer) ; Théobald : 375.

HOLOTYPE. Originally in Eidgenössische Technische Hochschule, Zürich, but cannot now be traced.

OTHER SPECIMENS. One specimen in Mus. Comp. Zool. Harvard, and another, described by Meunier, is believed to be in the Marseille Museum.

DISTRIBUTION. Miocene : Oeningen. Also reported from the Oligocene of Aix and the Oligocene of Cereste, Corent, Célas, France.

REMARKS. Heer's illustration is unsatisfactory. The thorax is very hairy, and some wing venation can be made out. One specimen only was described by Heer, from the Zürich collection, where however we have not succeeded in finding it.

Cockerell (1907), while investigating specimens in the Museum of Comparative Zoology, Harvard, came across an example of *Anthophorites mellona* Heer, from Oeningen, determined by Heer himself. Its venation could not be discerned. Since, however, some wing venation must have existed in Heer's original, this specimen cannot be the holotype. Cockerell (1909c) fixed *Anthophorites mellona* as the genotype.

Meunier's (1914) specimen from Aix-en-Provence was thought by him to belong to this species, though his description was meagre. He did, however, give photographs of two specimens. His pl. 6, fig. 5a is the specimen described; it appears to be well preserved. His pl. 6, fig. 5b is probably a photograph of Heer's *A. mellona* used for comparison, although no mention of this is given. Moreover, the resemblance between the two specimens is probably merely superficial.

The reports from the Oligocene are even more doubtful. They appear in Théobald's (1937) table, for each of the three localities. There is only a single specimen, however, and one *Anthophorites* is indeed known from the Oligocene of Corent, France, viz. *A. gaudryi* (p. 195). It is listed by Théobald under that fauna (1937: 433), but omitted from the list.

Anthophorites titania Heer 1849

- *1849 *Anthophorites titania* Heer: 99, pl. 7, figs 5a, b.
- 1856 *Anthophorites titania* Heer; Giebel: 183.
- 1891 *Anthophorites titania* Heer; Scudder: 687 (5926).
- 1907 *Anthophorites titania* Heer; Handlirsch: 891.
- 1909c *Anthophorites titania* (Heer); Cockerell: 315.

HOLOTYPE. Badische Landessammlung für Naturkunde, Karlsruhe, Inv.1273 (Oe.92).

PARATYPE. Eidgenössische Technische Hochschule, Zürich, No. Pl. I, 686 (not figured by Heer).

DISTRIBUTION. Miocene: Oeningen.

DESCRIPTION. The holotype has been examined, and found to have the head missing; the thorax is much distorted, and somewhat hairy. Both hind legs are in part preserved, one tibia and two basitarsi being very distinct. Both tibiae and basitarsi are broad and very hairy. The tibia is less well preserved but appears to be more than one and a half times as long as the basitarsus, without however being much broader. The abdominal segments are clearly visible and covered with long hairs. The basal vein is strongly curved at its base and soon straightens out. Length of abdomen 9 mm, width 5.5 mm.

The paratype, stated by Heer (1849) to have once been in the Karlsruhe Collection, is now at Zürich and has been examined by us. It was also studied by Cockerell (1909c) who considered its generic position to be obscure. This we hereby endorse.

The specimen is without head or legs, but the segmentation of the abdomen is clear. A few details of the thorax can be discerned: the pronotum is narrow, well margined but not quite reaching the tegulae; the mesonotum is prominent and arched, but rather small and well defined posteriorly by a transcutal suture; the mesoscutellum is clearly evident, the metathorax is delimited posteriorly by 'a sharp edge separating base from apical truncation', and a definite constriction exists between it and the abdomen. The wing venation has been almost effaced, but a distinct pterostigma still remains and a strong radius is present. Length of body (without head) 13.25 mm; length of thorax 4.25 mm, width 4.1 mm; length of abdomen 9 mm, width 5.25 mm; length of forewing 8 mm (as near as can be ascertained).

REMARKS. The shape of the basal vein of the holotype is a trait not uncommon in *Anthophora*, as the examination of many Recent specimens has revealed. It argues strongly against the alternative of assigning *A. titania* to *Halictus*. But the characters preserved do not permit us to be certain that the species is an *Anthophora sensu stricto*.

Anthophorites tonsa Heer 1849

- *1849 *Anthophorites tonsa* Heer: 99, pl. 7, figs 6a, b.
 1856 *Anthophorites tonsa* Heer; Giebel: 183-184.
 1891 *Anthophorites tonsus* Heer; Scudder: 687 (5927).
 1907 *Anthophorites tonsus* Heer; Handlirsch: 891.

HOLOTYPE. Badische Landessammlung für Naturkunde, Karlsruhe.

DISTRIBUTION. Miocene: Oeningen.

REMARKS. One specimen only has been described, and it cannot at the moment be found at Karlsruhe because of war damage. Heer's (1849) illustration is unsatisfactory.

Anthophorites veterana Heer 1849

- *1849 *Anthophorites veterana* Heer: 100, pl. 7, figs 7a, b.
 1856 *Anthophorites veterana* Heer; Giebel: 183-184.
 1891 *Anthophorites veteranus* Heer; Scudder: 687 (5928).
 1907 *Anthophorites veteranus* Heer; Handlirsch: 891.

HOLOTYPE. Eidgenössische Technische Hochschule (Lavater Collection), Zürich, No. 14.

OTHER SPECIMEN. Same collection, No. Pl. I, 684.

DISTRIBUTION. Miocene: Oeningen.

DESCRIPTION AND REMARKS. Heer's figure of the holotype agrees well with the holotype itself except that he omits the legs although he mentions them in the text. It is not well preserved. The insect was robust, with a broad convex mesoscutum. Tegulae prominent. The hind leg, particularly the basitarsus, is hairy and as broad as the tibia. On account of a depression in the rock which crosses the tibia, the relative lengths of the tibia and basitarsus are difficult to assess. Some venation

is present, but since the forewing overlies the hindwing, it is impossible to decipher it satisfactorily. The strong radius, however, is distinct and also some proximal portions of M+Cu and Cu. Length of body 14 mm; length of thorax 4.25 mm, width 5.5 mm; length of abdomen 8.75 mm, width 6.5 mm; forewing length 11 mm.

A second specimen (Pl. I, 684) labelled *Anthophorites* may tentatively be placed here. It is 12.5 mm long, extremely poorly preserved and black in colour.

Tribe MELECTINI Westwood 1840

DIAGNOSIS. Large, parasitic bees; clypeus of male black; posterior angle of mandible lies beneath middle of lower end of eye; first flagellar segment not unusually elongated; scopa absent; basitibial plates absent; claws with large inner basal lobe or tooth; middle tibial spurs unmodified; eighth tergum of the male usually feebly bilobate or bispinose and usually without a pygidial plate; seventh abdominal tergite of female with pygidial plate; seventh sternite of female somewhat produced, with the margins upturned to form a semitubular guide for the sting.

Pterostigma several times as long as broad, narrow, and not tapering beyond the base of vein r; marginal cell shorter than the distance from its own apex to the wing tip, broadly rounded apically, and usually not protruding beyond the last submarginal cell; normally three submarginal cells, the first usually longer than either of the others; second abscissa of vein M-Cu of posterior wings shorter than vein cu-a, sometimes virtually absent; jugal lobe of hind wing very small.

Genus *PROTOMELECTA* Cockerell 1908

*1908a *Protomelecta* Cockerell: 341.

1909b *Protomelecta* Cockerell; Cockerell: 81.

GENOTYPE. *Protomelecta brevipennis* Cockerell by monotypy.

REMARKS. According to Cockerell, 'A very *Melecta*-like genus but with the venation of the Eucerines and the large stigma of the Andrenids'. Special mention of the type was made by Cockerell (1909b).

Protomelecta brevipennis Cockerell 1908

*1908a *Protomelecta brevipennis* Cockerell: 341.

1909b *Protomelecta brevipennis*; Cockerell: 81.

1938 *Protomelecta brevipennis* Cockerell; Rodeck: 298.

HOLOTYPE. Univ. Colorado Mus., No. 18639.

DISTRIBUTION. Oligocene: Florissant.

REMARKS. The affinities of this species are by no means clear. It would appear to be an anthophorid, but its relationship with the melectines depends to some considerable extent on theoretical considerations only. A reinvestigation of the specimen is most desirable.

Family ANTHOPHORIDAE *incertae sedis*'*Anthophora*' *effossa* Heyden 1862

- *1862 *Anthophora effossa* Heyden : 76, pl. 10, fig. 10.
 1891 *Anthophora effossa* Heyden ; Scudder : 687 (5921).
 1907 *Anthophora effossa* Heyden ; Handlirsch : 890.
 1907 *Anthophora effossa* Heyden ; Cockerell : 228.
 1936 *Anthophora effossa* Heyden ; Statz : 260.

HOLOTYPE. British Museum (Natural History), 58781.

DISTRIBUTION. Oligocene : Rott.

REMARKS. It is necessary to distinguish between the '*Anthophora effossa*' of Cockerell (1907) which appears to be an ant (p. 202), and the *Anthophora effossa* Heyden which Cockerell apparently did not see. He maintained that Heyden's figure and description did not agree with his specimen, though whether he was sufficiently indulgent towards Heyden's work in this respect is not clear. Heyden's figures, however, are entirely useless for diagnostic purposes, and the holotype was damaged during the war, so that details are no longer recognizable. A further point to be noted is the very arbitrary way in which Heyden referred his specimen to *Anthophora*. For these reasons one is left with no alternative but to place it *incertae sedis*.

Anthophoridae gen. et sp. indet. 1

- 1856 *Anthophora* Latreille ; Menge : 26.
 1886 *Anthophora* ? Latreille ; Brischke : 278.
 1891 *Anthophora* ? Latreille ; Scudder : 686 (5919).
 1891 *Anthophora* ? Latreille ; Scudder : 686 (5920).
 1907 *Anthophora* ? Latreille ; Handlirsch : 890.

DISTRIBUTION. Eocene : Baltic amber.

REMARKS. Since Brischke had access to, and reported on, Menge's specimens, it is quite possible that Brischke refers here to Menge's *Anthophora*. Four specimens appear to have existed, though Menge mentioned only one.

Anthophoridae gen. et sp. indet. 2

- 1831 Hymenopt. aus der Fam. der Bienen ; Hünefeld : 2000 (i.e. 1100). (Specimens determined by Burmeister.)
 1891 (Apidae) Scudder : 682 (5873).
 1907 (Apidae) Burmeister ; Handlirsch : 892.
 1931 Apidae, Hünefeld ; Salt : 144.

DISTRIBUTION. Eocene : Baltic amber.

REMARKS. This entry has been wrongly attributed to Burmeister. It was merely the latter's list that was used by Hünefeld.

Superfamily APOIDEA (except Apidae) *incertae sedis*⁴**Apoidea** gen. et sp. indet. 1

- 1881a Apidae; Malfatti: 98.
 1891 (Apidae) Malfatti; Scudder: 682 (5874).
 1907 (Apidae) Malfatti; Handlirsch: 892.

DISTRIBUTION. Oligocene: Chiavone, Italy.

REMARKS. Poorly preserved.

Apoidea gen. et sp. indet. 2

- 1881 Apidae; Scudder: 290.
 1883 Apidae; Scudder: 280.
 1891 (Apidae—several) Scudder: 682 (5875).
 1907 (Apidae—mehrere) Scudder; Handlirsch: 892.

DISTRIBUTION. Oligocene: Florissant.

REMARKS. Scudder reported that several species occurred, 'most of them badly preserved; the largest appears to be a *Bombus*'.

Apoidea gen. et sp. indet. 3

- 1907 (? Apidae); Handlirsch: 893.

MATERIAL. ? Hofmuseum, Vienna (Bosniaski Collection).

DISTRIBUTION. Miocene: Gabbro, Italy.

REMARKS. Poorly preserved bee with short angulated antennae, habitus related to '*Apis melisuga*' (see p. 248).

Apoidea gen. et sp. indet. 4

- 1895 (Apidae n.g. resembling *Eucera*); Scudder: 122.
 1907 Apidae n.g. ? Scudder; Handlirsch: 890.

DISTRIBUTION. Miocene: Oeningen.

REMARKS. Some confusion exists over this entry. There are two difficulties. Firstly, according to Scudder (1895) and corroborated by Handlirsch (1907), this specimen may first have been considered a representative of *Bombus grandaevus*, but was later relegated to 'a new genus of Apidae, in which the neuration more closely resembles *Eucera*'. Secondly Cockerell (1908b) investigated a specimen, from Scudder's collection, which he referred to the genus *Calyptapis*. The doubt that arises here is whether or not Cockerell was referring to the entry of Scudder in his reference to a *Eucera* during his discussion of *Calyptapis*. See *Bombus florissantensis* (p. 212).

⁴ See also Appendix, p. 256.

Apoidea gen. et sp. indet. 5

1928 Apidae Leach ; Pongrácz : 156.

DISTRIBUTION. Miocene (Sarmatian) : Piski, Hungary.

MATERIAL. Magyar Állami Földtani Intézet, Budapest.

REMARKS. According to Pongrácz, the shape of the wings and the pointed abdomen indicate *Osmia* ; the large, contiguous eyes, however, point to *Apis*. Since only the male of *Apis* has contiguous eyes, whereas the pointed abdomen is not characteristic of the male, the specimen cannot be referred to *Apis*. On account of the general unreliability of the diagnoses of Pongrácz it is impossible to say to which group of insects the fossil belongs.

FOSSILS ERRONEOUSLY CLASSIFIED AS APOIDEA

(excluding Apidae)⁵

'Formicinae' (Meunier)

*1920 *Andrena tertiaria* Meunier : 730, pl. 1, fig. 4.

1931 *Andrena tertiaria* Meunier ; Salt : 145.

1936 *Andrena tertiaria* Meunier ; Statz : 260.

1936 Formicinen ; Statz : 260.

HOLOTYPE. Heimatmuseum, Siegburg an der Lahn.

DISTRIBUTION. Oligocene : Rott.

REMARKS. Venation largely effaced. Statz (1936) writes : 'Nach der Bildung des Kopfes und der Fühler, sowie der Thoraxsegmentierung und dem Bau der Beine gehört das Insekt gemäss der Ansicht von Bischoff, Berlin, zu den Formicinen.' [According to Bischoff of Berlin, this insect belongs to the formicoids on the basis of the structure of the head and antennae, as well as the segmentation of the thorax and leg anatomy.]

'Formicinae' (Cockerell) (*nec* Heyden)

1907 *Anthophora effossa* Cockerell : 228.

1907 'An Ant' ; Cockerell : 228.

DISTRIBUTION. Oligocene : Rott.

REMARKS. An ant, to be found among a series of specimens from Rott, in the Mus. Comp. Zool. Harvard.

Polistes kirbyanus Cockerell 1914

1909c 'Three species of *Osmia*' ; Cockerell : 316 (*partim*).

1909c A Wasp ; Cockerell : 316.

*1914 *Polistes kirbyanus* Cockerell : 638.

1914 *Osmia kirbyana* Heer MS ; Cockerell : 638.

⁵ See also Appendix, p. 257.

HOLOTYPE. Eidgenössische Technische Hochschule, Zürich, No. Pl. I, 68r, with counterpart.

DISTRIBUTION. Miocene: Oeningen.

REMARKS. The view is taken that among the 'three species of *Osmia*' referred to by Cockerell (1909c) as being at Zürich, one, the wasp, was called erroneously '*Osmia kirbyana*'. Not only was the generic identification wrong, but Heer appears to have given this specimen merely a manuscript name.

LARVAL CHAMBERS

'Genus' *CELLIFORMA* Brown 1934

*1934 *Celliforma* Brown: 539.

1935 *Celliforma* Brown: 527.

DIAGNOSIS. Fossil fillings of chambers purported to have been made by unknown digging or nest-building Hymenoptera.

GENOTYPE. *Celliforma spirifer* Brown 1934 by monotypy.

DISTRIBUTION. Cretaceous to Recent.

REMARKS. The name can hardly be maintained under the International Rules of Zoological Nomenclature, since it refers to objects made by animals, not to the animals themselves. It is used by Brown merely for the sake of convenience, in conformity with the practice adopted in palaeontology for fossil burrows, worm casts and footprints.

Celliforma favosites Brown 1941

*1941a *Celliforma favosites* Brown: 54, pl. 1, figs 1, 2.

1941 *Celliforma favosites* Brown; Bequaert & Carpenter: 51.

1941b *Celliforma favosites* Brown; Brown: 105.

HOLOTYPE. U.S. Geological Survey Collection.

DISTRIBUTION. Upper Cretaceous, Colorado and Montana Beds: Gunlock, south-west Utah, U.S.A.

REMARKS. Regarded by Brown as the comb of a wasp's nest resembling that of *Polistes*, but the possibility that it belongs to a social bee cannot be entirely dismissed. Bequaert & Carpenter (1941) questioned the correctness of Brown's determination, to which Brown (1941b) appears to have satisfactorily replied.

Celliforma spirifer Brown 1934

1934 Upper Eocene fossil molds; Brown: 534, fig. 3.

*1934 *Celliforma spirifer* Brown: 539.

1935 *Celliforma spirifer* Brown; Brown: 527.

HOLOTYPE. U.S. Geological Survey Collection.

DISTRIBUTION. Eocene, Bridger Formation: Wyoming, U.S.A.

REMARKS. This cell resembles that of an *Anthophora*, with a rounded base and a spiral seal. Brown, however, emphasizes that many anthophorid bees construct such cells, hence little systematic significance can be attached to these features, except that they render probable the existence of Anthophoridae or similar bees.

Celliforma germanica Brown 1935

1907 *Anthophora (Podalirius)* ? sp. Schütze : 25, pl. facing p. 56, figs 22, 23.

*1935 *Celliforma germanica* Brown : 527.

LECTOTYPE. Württembergische Naturaliensammlung, Stuttgart (Schütze's fig. 22), here selected.

OTHER SPECIMENS. Same collection, Schütze's fig. 23, and a third specimen referred to on p. 26.

DISTRIBUTION. Oligocene, Bunter Breccia : Wilhelm, Ries, Württemberg.

REMARKS. Schütze recognized these as burrows of Hymenoptera, and thought they belonged to a species of *Anthophora*, but it is impossible to assign them to any particular genus. It should be noted that they differ from *C. spirifer* and *C. nuda* in the presence of a slight waist-like constriction. A spiral lid is not preserved.

Celliforma nuda Brown 1935

1915 *Lithophaga nuda* Dall : 129, pl. 24, fig. 4.

1934 Lower Miocene fossil molds ; Brown : 534, fig. 1.

*1935 *Celliforma nuda* Brown : 527.

HOLOTYPE. U.S. Nat. Mus., No. 165187 or 165189 (Dall 1915 : pl. 24, fig. 4).

DISTRIBUTION. Lower Miocene, Silex beds of Tampa Limestone : Florida, U.S.A.

REMARKS. Originally described (Dall 1915) as molluscan boreholes, but recognized by Brown (1935) as hymenopterous. Dall had both molluscan shells of a *Lithophaga nuda* which he had described previously, and also burrows which he assigned to this species. Brown rightly identified as hymenopterous the burrow-filling figured by Dall ; hence it is the holotype of a species *Celliforma nuda* Brown (*nec* Dall).

The cell resembles that of *C. spirifer* Brown in its structure, including the spiral lid.

Celliforma bedfordi sp. nov.

(Pl. 1, figs 7, 8)

DIAGNOSIS. The innermost surface of the seal, that facing the main chamber, is distinctly spiral in structure, of at least five whorls, and is markedly concave.

HOLOTYPE. British Museum (Natural History), In.31434.

TYPE LOCALITY. Venus Bay, South Australia.

DISTRIBUTION. Pleistocene or Sub-Recent, calcareous travertine and consolidated dune-rock, coasts of south and west Australia.

REMARKS. Specimens of these chambers were obtained, in 1933, by the British Museum (Natural History) from Mr R. Bedford of Kyancutta Museum, South Australia. They differ from those described by Lea (1925) in that they are tubular, with septate cross walls, some 6-7 cm long by 2 cm in diameter. According to the correspondence of Mr Bedford, 'the prevalent type is only the main chamber of a structure of which the missing portion consists of a considerable number of small chambers separated by concavo-convex septa'. The latter, however, are believed to be the various layers of a single seal to the main chamber.

Celliforma septata sp. nov.

(Pl. 1, fig. 9 ; Pl. 2, fig. 1)

DIAGNOSIS. The innermost surface of the seal, facing the main chamber, is a plug which is not spiral. It appears to be just slightly convex. Seal composed of four septa.

HOLOTYPE. British Museum (Natural History), In.31435.

PARATYPE. Same collection, In.34133.

TYPE LOCALITY. Venus Bay, South Australia.

DISTRIBUTION. Pleistocene or Sub-Recent, calcareous travertine and consolidated dune-rock, south and west Australia.

REMARKS. These chambers appear to correspond to *C. bedfordi* n. sp. in size and shape, but differ in the form of the seal.

Celliforma sp. indet.

1932 'Tubular burrows in natural chalk'; Buxton : 3.

DESCRIBED SPECIMEN. British Museum (Natural History), Dept. of Entomology.

DISTRIBUTION. ? Bronze Age, not later than King Solomon, Megiddo, Palestine.

REMARKS. Perhaps made by *Osmia* or *Anthophora*, according to Buxton (1932). No seal described. A second group of 'mud nests', submitted by Mr P. L. O. Guy, Oriental Institute, Chicago University, was also mentioned by Buxton. This appears to be a group of puparia reminiscent of the Australian forms described by Lea (1925), but somewhat smaller and made of different material. The latter were reasonably assumed to be the work of beetles still living in the vicinity. No such conclusion can be hazarded of the organisms responsible for the 'mud nests' of Megiddo.

'Genus' *URUGUAY* Roselli 1939

Uruguay auranormai Roselli 1939

*1939 *Uruguay auranormai* Roselli : 73, figs 17-20, 22, 31(1-4).

1941 *Uruguay auranormai* Roselli ; Bequaert & Carpenter : 53.

1941b *Uruguay auranormai* Roselli ; Brown : 110.

DISTRIBUTION. Cretaceous or later : Uruguay.

REMARKS. Unfortunately the original work in which Roselli described the hymenopterous cells has not been seen, but it is fairly obvious that Bequaert & Carpenter's comparison of Brown's Cretaceous fossil, *Celliforma favosites* (p. 203), with *U. auroranormai* is far-fetched. It would appear from the descriptions of Bequaert & Carpenter (1941) and Brown (1941b) that the cells are not dissimilar to those described in the present work from south and west Australia and may well be the work of bees. Moreover, as Brown has pointed out, the fact that they occur in Cretaceous strata does not imply a Cretaceous origin for them.

V. SYSTEMATIC DESCRIPTIONS OF FOSSIL APIDAE

This section contains a detailed study of the fossil Apidae. The material is arranged according to tribes, and within them stratigraphically.

Family APIDAE Latreille 1802

DIAGNOSIS. Social bees, except possibly the tribe Euglossini (which has not so far been found in the fossil state) ; second flagellar segment much shorter than scape ; basitibial plates absent ; scopa of female, when present, forming a corbicula on each posterior tibia, except in queens of Meliponini ; inner apical margins of posterior tibiae of non-parasitic females, except in queens of Meliponini and workers of *Lestrimelitta*, provided with a tibial pollen rake ; pygidial plate absent ; wings hairy throughout, except possibly in a few fossil forms ; usually (and in all North American forms) the distance between the costal ends of the two recurrent veins is nearly twice as great as the length of the second recurrent vein, or even more, and is longer than the first recurrent.

CHALCOBOMBUS Group

Many fossil insects carry characters of such a type that their exact systematic position is difficult to define. Often new families, subfamilies and tribes are created for them but not infrequently this procedure defeats its own end by establishing units of separation where none exist. *Chalcobombus* embraces such a group and it seems to us inadvisable to erect a new tribe for it. This genus could be regarded as having affinities with the Bombini, or else it may have been the progenitor of *Sophrobombus* which we consider to be an ancestral Meliponine, and thirdly, it is not without affinity with the genus *Electrapis* which links it with the Apini. For these reasons we have not assigned a tribal name to the genus.

Genus *CHALCOBOMBUS* Cockerell 1908

*1908b *Chalcobombus* Cockerell : 327.

1909d *Chalcobombus* Cockerell ; Cockerell : 12.

GENOTYPE. *Chalcobombus humilis* Cockerell 1908, by subsequent designation of Cockerell (1909d : 11).

DESCRIPTION. Apidae of compact build, about 8 mm long; metallic tints sometimes in evidence; head broad, vertex usually with coarse, erect bristles, sparingly plumose, facial quadrangle variable; eyes not usually hairy, and ocelli large, close together, in a slight curve; scape comparatively long, flagellum variable in size; mouth parts elongate, 'tongue' hairy but slender with an apical circular flabellum; mandible with at least two marginal notches; abdomen subglobose; scutellum prominent and hairy; legs hairy, hind ones considerably plumose, pulvillus large, claws with short inner tooth; antenna cleaner with exceptionally long hairs, lining the notch or 'auschnitt', its clasp unusually large, fringed with very fine hairs along its inner surface, lacking a lobe, variable in size; along the distal margin of the hind tibia a crude rake of strong stiff setae, and flanking its anterior margin an inner tibial spur with one edge of stiff hairs, closely set. This spur is fairly closely pressed against the legs.

Forewing. Stigma distinct, slightly variable in size, triangular; marginal cell deepish, not particularly long; three subequal submarginal cells, the first sometimes the largest, but all three exhibiting variations in shape that are of specific value; second submarginal cell receiving first recurrent nervure beyond or near the middle; third submarginal cell receiving second recurrent nervure a short distance from its end; junction of cubito-anal cross vein and basal nerve coincident.

Hindwing. Cross vein cu-a somewhat oblique, or the upper half vertical; hamuli variable in number (8-11).

REMARKS. The genus was only mentioned in 1908 in a list of *Chalcobombus* species and in a genealogical tree. It was fully described in 1909. The above description is based entirely on Cockerell's published papers.

Chalcobombus hirsutus Cockerell 1908

*1908b *Chalcobombus hirsutus* Cockerell: 326.

1909d *Chalcobombus hirsutus* Cockerell: 12, text-fig. 8.

HOLOTYPE. Geological Museum, University of Koenigsberg.

DISTRIBUTION. Eocene: Baltic amber.

DIAGNOSIS. Head and thorax with long whitish hairs.

DESCRIPTION. A compact black bee, 8 mm long; head and thorax, particularly the scutellum, with long, white or yellowish hairs apparently intermixed with brown ones, and all sparingly plumose; face, particularly below, broad; scutellum conspicuously projecting; wings reddish-fuliginous; distal corner of second submarginal cell produced, third submarginal cell longer than second, narrowed more than half above.

Basitarsus as in *C. humilis*; legs with much coarse fuscous hair; flagellum is given as about 0.255 mm long and 0.170 mm thick, last joint 0.323 mm long.

REMARKS. This species was first listed with characters in 1908, but not fully described until 1909.

Chalcobombus humilis Cockerell 1908

*1908b *Chalcobombus humilis* Cockerell : 326.

1909d *Chalcobombus humilis* Cockerell ; Cockerell : 12, text-figs 6, 7.

1931 *Chalcobombus humilis* Cockerell ; Salt : 145.

HOLOTYPE AND PARATYPE. Geological Museum, University of Königsberg.

DISTRIBUTION. Eocene : Baltic amber.

DIAGNOSIS. Head and thorax above with short, black hair.

DESCRIPTION. Black, about 8.5 mm long ; head and thorax above with short, black hair ; vertex and front dull, with sparse, short, coarse, erect, black bristles, sparingly plumose ; second 'antennal joint' barrel-shaped ; wings dark fuliginous ; stigma triangular and distinct, marginal cell ending rather obtusely away from costa and possessing a small appendiculation ; second submarginal cell greatly narrowed above, narrower on marginal than is the third ; third submarginal cell narrowed at least half above.

Basitarsus squarish ; flagellum a little variable in size and possibly in thickness - Cockerell quotes lengths of 1.955 mm and 2.125 mm, and thickness 0.187 mm.

REMARKS. This species, selected by Cockerell (1909d) as the genotype, was first listed with characters in 1908 but not fully described until 1909.

Chalcobombus martialis Cockerell 1908

*1908b *Chalcobombus martialis* Cockerell : 326.

1909f *Chalcobombus martialis* Cockerell ; Cockerell : 22.

1931 *Chalcobombus martialis* Cockerell ; Salt : 145.

HOLOTYPE. Geological Museum, University of Königsberg.

DISTRIBUTION. Eocene : Baltic amber.

DIAGNOSIS. Head, mesothorax and scutellum dull black, prothorax and tubercles coppery red.

DESCRIPTION. About 8 mm long ; mesothorax, scutellum and vertex dull black, but prothorax and tubercles coppery red ; face and abdomen black but legs metallic copper-red or crimson, moreover, the hind margins of the segments very narrowly but conspicuously silvery white, the dark part next to the margins stained with red, especially on the first segment ; scape shortish ; hind basitarsus twice as long as broad ; third submarginal cell is broad above ; first recurrent nervure joins second submarginal cell near middle ; wings pale reddish brown ; stigma large but not of great width ; second recurrent nervure with strong double curve.

Thick-set bee ; pubescence black or dark fuscous, not abundant ; the antennal joints appear to be known with some precision, as follows : third longer than second, fourth very short, about twice as broad as long, fifth conspicuously longer than fourth.

REMARKS. This species was listed with characters in 1908, but not fully described until 1909.

Tribe **BOMBINI** Latreille 1802

DIAGNOSIS. Moderate-sized to large hairy bees; clypeus slightly protuberant, its lower lateral portions being slightly bent backward; malar space long; labrum about twice as broad as long; proboscis usually not reaching beyond middle coxae; scutellum rounded; posterior tibiae of male neither swollen nor fossate; two posterior tibial spurs always present; pterostigma often small, not tapering beyond base of vein r; apex of marginal cell separated from wing tip by a distance equal to at least half of cell; jugal lobe of hindwing becoming reduced or absent.

REMARKS. No primitive forms are known of this tribe, the earliest appearing in the Oligocene (Aquitanian), and these are poorly preserved. The first convincing bumble bees are of Oligocene age, from Florissant. [For *Probombus* see Appendix, p. 256.]

Genus **BOMBUS** Latreille 1802

*1802a *Bombus* Latreille: 437.

1906 *Calyptapis* Cockerell: 42 (Genotype *Calyptapis florissantensis* Cockerell 1906 by monotypy).

1908b *Calyptapis* Cockerell; Cockerell: 324.

GENOTYPE. *Apis terrestris* Linnaeus 1758 [ICZN Opinion 220, 1954].

DIAGNOSIS. Moderate-sized to large hairy bees; clypeus slightly protuberant; female with well-developed corbicula on each hind tibia, the latter also possessing two strong spurs but no developed comb.

Basitarsus rectangular, strongly developed and inner surface covered with strong coarse bristles; depstum or auricle present. Posterior tibia of male flattened but without corbicula.

Bombus crassipes Novak 1877

*1877 *Bombus crassipes* Novak: 92, pl. 3, fig. 4.

1891 *Bombus crassipes* Novak; Scudder: 690 (5951).

1907 *Bombus crassipes* Novak; Handlirsch: 891.

1928 *Bombus crassipes* Novak; Wheeler: 97.

1931 *Bombus crassipes* Novak; Cockerell: 309.

1936 *Bombus crassipes* Novak; Statz: 260.

HOLOTYPE. Whereabouts unknown.

DISTRIBUTION. Oligocene (Aquitanian): Krottensee, Bohemia.

DESCRIPTION. Length of body 10 mm, width 6 mm; dark brown in colour, densely hairy; hind legs strongly developed, very hairy; auricle possibly not so well developed; femurs of hind legs thick; tibiae flat, widening posteriorly and truncated; basitarsus large, flat and truncated at both ends.

REMARKS. One specimen only, not well preserved, neither head nor wings being discernible. Fortunately Novak's description is helpful. It suggests that the specimen was a genuine *Bombus*. The figure, however, is very bad and possibly incorrect

since three hind legs are displayed. What may be the right hind leg is in the correct position, and except for the omission of the auricle and the tibial spurs is remarkably reminiscent of *Bombus*. Of the left hind leg, the basitarsus only is satisfactorily preserved. This, too, is *Bombus*-like. The third 'leg' is depicted in an anterior position where in fact the wing might be expected; perhaps only a mass of chitin is intended, which has been given the semblance of a basitarsus by the artist. The hind leg is very hairy and the corbicula is clearly indicated.

***Bombus abavus* Heer 1867**

(Pl. 2, fig. 2)

- *1867 *Bombus abavus* Heer : 5, pl. 3, figs 9, 10.
- 1891 *Bombus abavus* Heer ; Scudder : 690 (5948).
- 1907 *Bombus abavus* Heer ; Handlirsch : 892.
- 1909c *Xylocopa abavus* (Heer) ; Cockerell : 314.
- 1928 *Bombus abavus* Heer ; Wheeler : 97.
- 1928 *Xylocopa abavus* (Heer) ; Wheeler : 97.
- 1931 *Bombus abavus* Heer ; Cockerell : 309.
- 1931 *Xylocopa* Cockerell : 309.
- 1938 *Bombus abavus* Heer ; Armbruster : 87.

HOLOTYPE. Said to be in Eidgenössische Technische Hochschule, Zürich, but no trace can be found in that collection, and it must be presumed lost.

MATERIAL. Two specimens in the Eidgenössische Technische Hochschule, Zürich (Nos. Pl. I, 808, examined by Cockerell, and SN.201) ; one specimen in the Badische Landesammlung für Naturkunde, Karlsruhe (No. Inv.1268) (Oe.90).

DISTRIBUTION. Miocene, Oeningen.

DESCRIPTION AND REMARKS. Cockerell and Armbruster, who did not examine the type, were inclined to place this species in *Xylocopa*, possibly because of Heer's remark that the basitarsus is hairy. The venation, however, which Cockerell wrongly maintained could not be made out, is somewhat like that of *Bombus* in specimen No. Pl. I, 808. Moreover, the 'globular' abdomen of specimen SN.201 is not a feature of *Xylocopa*. In the circumstances it is advisable to retain this form in the genus in which it was originally placed, but its systematic position remains uncertain. The three existing specimens may be described as follows.

Specimen Pl. I, 808. Only thorax and legs are preserved with parts of the wings, especially the greater part of one forewing. The basal vein is fairly long, and its posterior segment is much longer than its anterior segment; cross vein cu-a is slightly distad of junction of basal nerve with Cu; second recurrent nerve is angular shortly before it meets the base vein of the second submarginal cell. The last recurrent nerve is incompletely preserved, and the junction lies in the proximal half of this vein.

The wing differs from that of *Xylocopa* in that the anterior segment of the basal vein, although short, is not so short as is usual for this genus, secondly in the comparatively slightly greater length of the basal vein, and thirdly in the fact that the

second recurrent nerve meets the base vein of the second submarginal cell well away from its apex. In these characters it resembles *Bombus*.

Forewing length at least 6.5 mm. The legs,⁶ particularly the hind ones, are stout and hairy but not so much as to warrant the exclusion of the species from *Bombus*. The broad thorax reveals substructures of the notum, which was not without hairs. Length of thorax 4 mm, width 5.5 mm.

Specimen SN.201. Head not preserved. The fossil consists of thorax and abdomen with parts of legs, and the merest trace of a wing. The thorax and abdomen are hairy and there is a strong suggestion of hairs on the legs. Since the type figured by Heer indicated an insect which had part of the head and several legs present, it is obvious this is not Heer's type. Length of thorax 4 mm, width 5 mm; length of abdomen 6 mm.

Specimen Inv.1268 (Oe.90). This specimen was identified on the label as *Xylocopa senilis*. Like the other known fossils referred to this species (p. 191) it is poorly preserved, lacking head, part of thorax, and all legs except one hind femur and tibia. The abdomen, however, is complete, and the hairs and segmentation very distinct. Moreover, wings are present, that on the right showing some important features of the venation. Dimensions: length of abdomen 10.5 mm, width 7 mm; length of forewing 10 mm; length of hind tibia 3.5 mm. It is thus clear that the specimen is larger than the other known specimens of *B. abavus*, but since bumble bees vary much in size, this is no reason for excluding it from the present species.

Diagnostic characters are seen in the shape of the marginal cell, particularly in the concavity of its base, which in *Xylocopa* is convex and very acute proximally, in the position of the insertion of the first submarginal cross vein (abscissa Rs) on the posterior margin of the marginal cell which is much more distal in *Xylocopa*, and also in the curve, or rather indentation, of the cubitus just prior to its distal splitting into Cu₁ and Cu₂, a character much less prominent or lacking in *Xylocopa*. These are not conclusive arguments for placing the specimen in the genus *Bombus* rather than *Xylocopa*, but since in addition the long tibia has strong hairs arranged in a manner suggesting a corbicula, the evidence becomes overwhelming. That femur and tibia are preserved, rather than tibia and basitarsus, is proved by the angle between them. The basitarsus, indeed, is present also but only very incompletely preserved; superficially it resembles the distitarsi. Its erroneous interpretation as distitarsi no doubt contributed to the earlier identification of the specimen with *Xylocopa*.

The colour of the chitin and hairs is dark brown. Hairs are very conspicuous on the apex of the abdomen but become much sparser on the base of the abdomen and the thorax. Markings on the thorax indicate the presence of morphologically distinct regions, but these are too poorly preserved to be of use for generic identification.

⁶ Cockerell (1931) maintained, 'The legs show a scopa, and the hind tibia is very broad, with a gently curved longitudinal ridge visible on both sides, and, therefore, certainly natural. This ridge is normal for *Xylocopa*, to which *Bombus abavus* Heer must apparently be referred'. This ridge, however, could quite well, in part, be the outline of the corbicula of a *Bombus*, and in any case would almost certainly have been masked by the scopa in a fossil *Xylocopa*.

Bombus florissantensis (Cockerell 1906)

1895 Apidae n.g. ; Scudder : 122.

*1906 *Calyptapis florissantensis* Cockerell : 42.

1907 *Calyptapis florissantensis* Cockerell ; Handlirsch : 890.

1908b *Calyptapis florissantensis* Cockerell ; Cockerell : 324, 326.

1909b *Calyptapis florissantensis* Cockerell ; Cockerell : 80.

1931 *Calyptapis* Cockerell ; Cockerell : 311.

HOLOTYPE. Mus. Comp. Zool. Harvard, No. 2008 (= Scudder Coll. No. 4933).

MATERIAL. Specimen studied by Cockerell (1908), from the Oligocene shales of Florissant.

DISTRIBUTION. Oligocene : Florissant.

DIAGNOSIS. Length of body 15 mm ; length of anterior wing 8.5 mm ; head and thorax black but abdomen rather pale reddish, the junctions of the segments distinguished by moderately broad, light bands ; although legs are hairy, as in *Bombus*, and the hind legs exhibit a corbicula, the abdomen is not noticeably hairy, and the inner tooth of the bifid claws is much smaller and shorter.

Wings hyaline, with pale veins, cubito-anal cross vein (cu-a) of forewing vertical except where it bends away immediately prior to the junction with basal nerve. It differs from Recent *Bombus* 'in the form of the third submarginal cell and in the somewhat less specialised second submarginal' (Cockerell 1908b).

Stout-bodied, like Recent *Bombus* ; hind basitarsus flattened and quadrate, with hairy margins. It is stated to be 'broadly emarginate apically'.

REMARKS. The above description is based on Cockerell's of 1908. He placed the specimen in the genus *Calyptapis* because of the peculiarities of the second and third submarginal cells. Apart from the vagueness of his statement, however, it is precisely at this part of the wing that variation might be expected in an Oligocene species. The erection of a new genus indeed appears to confuse the issue, for it seems to us that we are here dealing with a perfectly legitimate *Bombus* able to bear the most detailed comparison with Recent forms.

Formerly Cockerell regarded it as near *Melissodes* (Anthophoridae), but since 1908 as one of the Bombini. He apparently based his first description on a poorly preserved specimen already referred to *Eucera* by Scudder (1895), who said it was 'an insect which may possibly be *Bombus grandaevus* Heer, but which belongs to a new genus of Apidae, in which the neuration more closely resembles that of *Eucera*'. Later, a better specimen was discovered which clearly indicated the relationship with *Bombus*.

Bombus proavus Cockerell 1931

*1931 *Bombus proavus* Cockerell : 309, pl. 1, fig. 8.

1936 *Bombus abavus* Cockerell ; Statz : 295.

HOLOTYPE. Mus. Comp. Zool. Harvard, No. 2940a, b.

DISTRIBUTION. Miocene, Latah Formation ; near Spokane, Washington, U.S.A.

DIAGNOSIS. A robust insect, with long black hair, at least on the face ; forewing 15 mm long ; basal vein slightly proximal of junction of vein cu-a ; first submarginal cross vein (abscissa Rs) not angulate ; first marginal cell on first media cell slightly longer than second submarginal on same cell ; second submarginal cell on the marginal cell very little longer than the third on same cell ; lower side of third submarginal conspicuously bent at insertion of second recurrent ; wing hyaline, slightly brownish, the upper part of the marginal cell moderately infuscated.

REMARKS. Insect known from Cockerell's description and figure. Its body is so crushed that most features are obliterated, but the forewing is in an excellent state of preservation. As with *B. florissantensis* (Cockerell) the third submarginal cell in this specimen differs from Recent *Bombus*.

According to Cockerell this was the first true fossil *Bombus* to be described, and all other species belong to other genera or are of doubtful reference to *Bombus*. He also maintains that it is 'nearest to European *B. lapidarius*'. Statz (1936) when referring to this specimen erroneously named it *B. abavus*.

Tribe MELIPONINI Handlirsch 1924

DESCRIPTION. Moderate-sized to minute bees, in perennial colonies ; Recent forms with eyes bare, sparsely hairy in some queens ; labrum much broader than long ; epistomal suture arched upward, as in *Apis*, close to the antennal sockets, and the clypeus not protuberant.

Posterior tibial spurs reduced or absent ; tibial comb always present in Recent forms (*Lestrimelitta* excepted) and distinct ; in fossil forms if a comb is not present there is always an inner but modified tibial spur. Basitarsus very rarely as broad as tibia ; auricle or true depstum apparently always absent, while the inner surface of the basitarsus may not have the whole area completely covered with strong bristles ; claws of Recent females simple.

Ninth sternum of male virtually absent, being represented, if at all, by a narrow, longitudinal, weakly sclerotic band beneath the genitalia ; eighth sternum rather narrow, having the form characteristic of the ninth in most bees ; sting reduced.

Wings extending beyond the body ; marginal cell often open, and forewing with veins always weak (or weakening) distally ; pterostigma of moderate to large size, extending well beyond base of vein r ; jugal lobe of hindwing present.

REMARKS. The genus *Sophrobombus* is represented by fossil forms, but not *Melipona*. The tribe ranges from Eocene to Recent and is today widely distributed in the tropics. Many are found in East African copal.

Genus *SOPHROBOMBUS* Cockerell 1908

*1908b *Sophrobombus* Cockerell : 327.

1909f *Sophrobombus* Cockerell ; Cockerell : 21.

GENOTYPE. *Sophrobombus fatalis* Cockerell 1908, by monotypy.

DIAGNOSIS. Small bees resembling *Chalcobombus*; mandibles with at least a convex cutting edge; ocelli large and arranged in a curve.

Basitarsus flattened, quadrangular, short, having on the inner surface a small, bristleless area around the posterior apex; a ridge of short hairs exists on the inner surface of the hind tibia; inner hind tibial spur present, fringed with hairs along one edge, and acting as a 'stop' to the pollen rake.

Forewing with second submarginal cross vein absent; basal vein going basad some distance from vein cu-a; pterostigma well developed; marginal cell possibly slightly open at apex.

REMARKS. Cockerell considered this genus to be a near descendant of *Chalcobombus*. It differs from it, however, in a number of points, particularly in the reduction of the wing venation. In this respect it is much nearer *Trigona* which it closely resembles in habitus, as well as in the hairless patch on the inner surface of the basitarsus and the ridge on the inner surface of the hind tibia. There seems little doubt therefore that it could have been an ancestor of the Meliponini. The presence of the inner tibial spur, rather than hindering this view, fosters it.

The genus was first mentioned by Cockerell (1908) in a list of Baltic amber species and in a genealogical tree. It was fully described in the following year.

Sophrobombus fatalis Cockerell 1908

(Pl. 2, figs 3, 4)

*1908b *Sophrobombus fatalis* Cockerell: 326.

1909f *Sophrobombus fatalis* Cockerell; Cockerell: 21.

1931 *Sophrobombus fatalis* Cockerell; Salt: 146.

HOLOTYPE. Geological Museum, University of Königsberg.

MATERIAL. Scheele Collection, No. 1225, in Geologisches Staatsinstitut, Hamburg.

DISTRIBUTION. Eocene: Baltic amber.

DIAGNOSIS. Length 8-8.5 mm. Short, thick-set insect, metallic dark coppery-red, almost without pubescence. Vertex with very short fuscous plumose hair. Mandibles broadened apically, with a convex cutting edge; clypeus weakly punctate; scape comparatively long and curved. Thorax above with erect, strongly plumose fuscous hair, twice as long on scutellum as on mesothorax; scutellum projecting. Hind tibia long and large; hind basitarsus quadrangular, less than twice as long as broad, the outer angles acute. Claws with an inner tooth a little beyond the middle.

DESCRIPTION. Cockerell gave the following description of the specimen: 'Mandibles (apparently without visible teeth) with long and short bristles on the lower margin; blades of maxillae long and slender; antennae very much closer together than either is to the eye, second joint barrel-shaped, but its basal third narrower and cylindrical, third joint much longer than fourth but not quite so long as second, fourth broader than long; legs moderately clothed with fuscous hair; pulvillus large; 2-4 tarsal joints, small, cordiform; wings pale fuscous, veins and stigma dark brown; hind wing with vein cu-a a little oblique, with the lower endmost apicad.' We have examined specimen no. 1225 and find that it agrees closely with

the above description, except that the second flagellar joint, i.e. third antennal joint, is somewhat longer than the first. This does not, however, justify creating a new species. The detailed description of this new specimen is as follows.

A metallic, coppery-red insect, not hairy. Overall length, from head to wing tip, 8.5 mm; the actual body, however, is shorter, with an overall length from head to the tip of the abdomen of only 6 mm. The extent of wing overlap is thus considerable but was possibly somewhat less in the living creature since the whole abdomen is compact, which suggests considerable contraction. Other approximate measurements are: width of thorax 2.75 mm, length 2.5 mm; width of head 2 mm, length 1.25 mm; length of tibia 2.5 mm.

Head. The rather large head is not preserved in its entirety since a hollow occurs in the amber near the mouth parts, and some 'schimmel' also has developed here. The upper part, however, is distinct. The compound eyes appear to be naked; the vertex is covered with fuscous hair, possibly plumose; ocelli are large and prominent, set in a broad shallow triangle; malar space quite broad but short, if the limits of observations are the actual limits of this region; one antenna quite distinct, inserted on the lower half of the face; scape well formed, curved; basal segment of flagellum, i.e. the pedicel, barrel-shaped, second slightly larger than first, but tapering basally, third the shortest, broader than long but not much shorter than the fourth segment, the terminal segment the largest, at least twice the size of the remaining segments which are equal in shape and size. Eleven flagellar segments are present.

Thorax above indistinct owing to cracked amber and some 'schimmel'. It was apparently well arched and covered with hairs which extended somewhat down the sides. The projected scutellum can be observed.

Abdomen. Ovoid in shape. Although the tip of the abdomen can be seen very distinctly, there is no trace whatever of a sting.

Legs. Only the hind legs have been sufficiently preserved for study. They are remarkable for the great length of the tibia with a shallow scoop-like extension overlapping the base of the basitarsus on the outside, and the comparatively small, quadrangular basitarsus, not much longer than broad, with the posterior distal angle strikingly acute. In detail, the hind leg has the following characters.

Tibia. Corbicula present with the usual scopa, some hairs of which may be slightly plumose; the corbicula itself relatively free from hairs; the inner surface of the tibia exhibits, posteriorly, a longitudinally arranged plateau-like region of short close hairs, occupying a third of its area and extending slightly to the femur, and bounded (though seen only under certain lighting conditions) by a dark rim which is quite broad towards the base of the femur but narrow on the tibia except for a broader zone at the pollen rake. Two appendages are to be found on the tibia, a strong pollen rake and an inner tibial spur, the latter having become modified to carry a blade of fine hairs, as though developing into a comb. That it is not the latter is clear from its position on the inner surface of the tibia where it forms a 'stop' to the pollen rake. It also differs from the typical spur by being more closely pressed against the leg and more intimately associated with the pollen rake.

Basitarsus. The inner surface exhibits a well-developed pollen brush, consisting of seven rows of strong bristles, with possibly 18–20 bristles to the middle rows, though the latter number is difficult to ascertain with complete accuracy owing to pollen clogging the brush. Apical and basal rows have at least four bristles less in consequence of the development of small, bristleless areas around the posterior apices.

Pulvillus large; claws bulbous at base and strong, with very small tooth beyond half-way; remaining tarsal joints cordiform.

Wings. Fuscous, hairy, and rather more elongate than is normal for the Baltic amber bees. A study of the venation of the forewing reveals the absence of the second cross vein of the submarginal cells; the basal vein becoming basal a short distance away from vein cu-a;⁷ the latter vein a little oblique, the posterior end most apicad; stigma well developed; marginal cell pointed; second submarginal cell shorter than slightly open marginal; second recurrent vein weak and sloping strongly basad. Since the forewings are folded along the back of the insect, the hindwings are not visible.

REMARKS. The absence of reference by Cockerell to denticles on the mandible cannot be taken too seriously since such denticles, unless very prominently displayed on an open mandible, are not easy to see. Cockerell's specimen was listed with characters in 1908, but not fully described until 1909.

Genus *TRIGONA* Jurine 1807

*1807 *Trigona* Jurine: 246.

1896 *Meliponorytes* Tosi: 352 (type species *Meliponorytes succini* Tosi).

GENOTYPE. *Apis amalthea* Olivier 1789, by subsequent designation of Latreille (1810: 439).

DIAGNOSIS. Stigma well developed, rounded below; wings relatively long, extending beyond apex of abdomen; hamuli about five or six, rarely more than nine or fewer than four; body length from 2 to 8 mm, rarely exceeding 11 mm.

REMARKS. The genus *Meliponorytes* was erected by Tosi (1896) to embrace forms ancestral to Recent *Meliponini*. All the fossils so far discovered and which have recognizable descriptions, however, are believed to be referable to *Trigona*. But the creation of the new genus *Meliponorytes* for what is apparently a genuine *Trigona* must have been a deliberate procedure, since Tosi makes mention of the likeness of his specimens to *Trigona* and also to the subgenus *Tetragona*. *Meliponorytes* was thus undoubtedly erected on account of those slight uncertainties attending fossil forms, although the action here seems scarcely justifiable. Tosi's descriptions and illustrations have been very carefully studied and there seems little doubt that his *M. succini* (see p. 221) is definitely a *Trigona* of the subgenus *Tetragona*, whilst the subgenus cannot be stated for his *M. sicula* (p. 224). Kerr & Maule (1964) thought

⁷ Not, as stated by Cockerell for his specimen, a considerable amount, though it is the most we have noticed among Baltic amber bees.

that *M. succini* belonged to *Meliponula*, but in a different subgenus from *M. boccandei*.

It will be recalled that all *Trigona* species lack hind tibial spurs, yet all, except *Lestrimelitta*, possess the hind tibial comb. The variations of the basitibial surfaces are of subgeneric value. [For subgenus *Nogueirapis* see Appendix, p. 257.]

Subgenus *TRIGONA* Jurine 1807

*1807 *Trigona* Jurine : 245.

GENOTYPE. *Apis amalthea* Olivier 1789.

DIAGNOSIS. (From Schwarz 1948.) Mandible toothed usually from end to end along its apex, or with three teeth on at least the outer two-thirds of the apex and an angulation at the inner extremity. Hind tibiae a little longer than the combined length of their femora and trochanters. The fringe along the posterior lateral contour of the hind tibiae with plumose hairs in addition to the usually sparser simple hairs. The base of the inner face of the hind basitarsi with a differentiated, more or less oval, area of appressed hairs that contrast with the brush-like hairs on the apical half to two-thirds of this inner face.

REMARKS. At least one fossil form is so far known, from the Pleistocene.

Trigona (Trigona) erythra Schletterer 1891

*1891 *Trigona erythra* Schletterer : 2.

1895 *Melipona togoensis* Stadelmann : 620.

1948 *Trigona erythra* var. *togoensis* Stadelmann ; Schwarz : 51, 61, 68, 132.

1961 *Axestotrigona erythra* (Schletterer) ; Moure : 239.

1961 *Axestotrigona togoensis* (Stadelmann) ; Moure : 239.

FOSSIL SPECIMEN STUDIED. British Museum (Natural History), In.17664.

DISTRIBUTION. Pleistocene : East African copal ; and Recent.

DESCRIPTION. Body length 5.75 mm ; general colour brownish-black to black. Head broader than thorax, hairs upright and relatively strong on vertex, ocelli prominent, in a gently curved line, hind ocelli more distant from each other than from compound eyes ; from the front ocellus there runs a prominent frontal line ; face, particularly the clypeus, appears to be covered with a close white pubescence ; length of scape little more than half the length of the flagellum, and all flagellar segments, except the last, not longer than broad, the last being longer than broad, and pointed.

Thorax markedly triangular, black, its surface matt, probably due to a short pubescence and to very fine rugosity ; longitudinal line through scutum (median mesoscutal line) masked by a crack in the amber, but the polished and shining furrow between scutum and scutellum can just be recognized ; scutellum clearly projecting, with strong chitinized hairs on its ridge.

Abdomen dark in colour with only few traces of brown, anterior segments smooth and shiny, hind segments covered with short pubescence ; legs on the whole black

but not sufficiently well preserved at extremities to judge whether the latter are brown (most have been cut off short at the edge of the copal) ; corbicula well formed, wide, neatly hollowed, inner surface difficult to see ; one basitarsus detached, the other wanting ; claws not notched.

Marginal cell of forewing a little open at apex ; one rather weak submarginal cross vein ; first recurrent distinctly angular before junction with vein M ; seven hamuli.

REMARKS. No diagnosis is given because the taxonomic position of the Recent species is still *sub judice*, and we are not sufficiently acquainted with previous investigations concerning this group to be able to make a useful contribution.

The fossil agrees with Recent specimens of *Trigona togoensis* Stadelmann in the British Museum (Natural History) and our description of the fossil agrees in all essential respects with the original description of *T. togoensis* by Stadelmann.

The two Recent forms *T. togoensis* and *T. erythra* differ in the colour of the abdomen, which is rusty red in the latter. *T. togoensis* is also slightly smaller. Schwarz, however, regards these differences at best as of varietal value, and we have followed him in regarding them as races of a single species. In the colour of the abdomen, the fossil from East Africa agrees with the West African form *T. togoensis*.

Subgenus *Hypotrigona* Cockerell 1934

- *1934 *Hypotrigona* Cockerell : 54.
- 1961 *Liotrigona* Moure : 223 (type species *Trigona bottegoi* Magretti).
- 1961 *Hypotrigona* Moure : 220.

GENOTYPE. *Trigona gribodoi* Magretti 1884, by original designation.

DIAGNOSIS. Minute bees, with dull tegument but without true yellow marks. Clypeus flat, a little wider than twice its length and one-third as long as clypeocular distance. Lateral portion of epistomal suture straight. Mandible bidentate. Scape short. Flagellar segments very short. Bifurcation between M and Cu after cu-an. Submarginal angle about 90°. Hind basitarsus about twice as long as broad. [See also Appendix, p. 256.]

Trigona (Hypotrigona) gribodoi Magretti 1884

(Pl. 2, figs 5-7)

- *1884 *Trigona gribodoi* Magretti : 630.
- 1894 *Trigona braunsi* Kohl : 280.
- 1895 *Trigona bottegoi* Magretti : 156.
- 1934 *Trigona (Hypotrigona) gribodoi* Magretti ; Cockerell : 54.
- 1934 *Trigona (Hypotrigona) bottegoi* Magretti ; Cockerell : 55.
- 1961 *Hypotrigona gribodoi* (Magretti) ; Moure : 220.
- 1961 *Liotrigona bottegoi* (Magretti) ; Moure : 223.
- 1964 *Trigona (Hypotrigona) gribodoi* Magretti ; Kerr & Maule : 7.
- 1964 *Trigona (Liotrigona) bottegoi* (Magretti) ; Kerr & Maule : 7.

SPECIMENS STUDIED. British Museum (Natural History), In.38982-38993, In.17686, In.18209, In.18214, In.18220, In.18226, 585II, 58622.

DISTRIBUTION. Recent (common in Africa); Late Pleistocene: East African copal.

DIAGNOSIS. Length of body not exceeding 4 mm; head and thorax black, abdomen and eyes dark brown. There is no apparent natural testaceous coloration of the scape, mandibles or anterior legs. The body is only sparsely haired except, chiefly, for the ridge of the scutellum and the basitarsi; hind tibia triangular, neither clavate nor club-shaped, the inner face showing an elevated plateau-like area with a posterior rim.

DESCRIPTION. Face round, black; antennae of only moderate length, flagellum broad and shortish; ocelli prominent. Although the whole face appears uniformly black, the copal is believed to mask its short white pubescence, except in In.38993. The same is true of the hairs on the black thorax, but the stronger, more heavily chitinized hairs of the scutellum can be distinguished. Hind tibia not copiously haired, and because the hairs are fuscous they are sometimes difficult to see. All the tarsi appear to be more strongly haired than the tibiae. Wings hyaline; hamuli five or six, stigma well developed, marginal cell open at apex, no submarginal cross veins in evidence, except sometimes a stump for the first.

Some specimens show a very strongly reduced venation particularly of the posterior apical region of the forewing. The yellow rim to the compound eyes, so often noticeable in copal specimens, is believed to be due to the medium of their preservation.

REMARKS. The following are brief statements on the insect inclusions of each numbered piece of copal preserved in the British Museum collection. The first twelve pieces come from the Luke Thomas Collection.

In.38982. One typical *T. (Hypotrigena) gribodoi*, and also a second inclusion of an insect believed to be a termite but whose head and thorax have been removed during the polishing of the copal.

In.38983. A well-preserved specimen of *T. (H.) gribodoi*, with quite a dark abdomen.

In.38984. Eight insect inclusions, i.e. six *T. (H.) gribodoi*, one dipteran and one termite. Some are most excellently preserved, and one of the bees shows an advanced reduction of the veins of the forewing.

In.38985. One *T. (H.) gribodoi* and various other chitinous remains of insects, including aculeates. The bee is poorly preserved, portions of it having been worn away during the polishing of the copal, but sufficient remains for it to be identified.

In.38986. Two *T. (H.) gribodoi*, both well preserved.

In.38987. Copal too cracked for accurate diagnosis, but contains one insect which appears to be a *T. (H.) gribodoi*.

In.38988. A poorly preserved specimen of *T. (H.) gribodoi*. Copal around the insect somewhat cracked. A second inclusion, again rather poorly preserved, but markedly petiolate, is believed to be an ant of the genus *Crematogaster*.

In.38989. A *T. (H.) gribodoi*, well preserved.

In.38990. A well-preserved *T. (H.) gribodoi*, and a second unidentifiable inclusion.

In.38991. Two *T. (H.) gribodoi*, one very well preserved, the other somewhat less so, on account of its position on the edge of the piece of copal, which is slightly cracked.

In.38992. One well-preserved *T. (H.) gribodoi*.

In.38993. Two *T. (H.) gribodoi*, one better preserved than the other. Here the pubescence, so characteristic of the species, is plainly visible. Both show a little coating of hair.

58511. All six insect inclusions appear to be *T. (H.) gribodoi*. In copal stated to be from Stettin on the Baltic, purchased from J. C. Rees 1867. There is, however, strong evidence from the so-called 'Baltic copal' from Stettin was imported from East Africa.

In.17686. Two *T. (H.) gribodoi*. Copal: East Africa.

The characters of the following specimens agree more with the original description of *T. bottegoi* Magretti than with *T. (H.) gribodoi* Magretti. Unfortunately, our study of Recent and fossil material leads us to believe that the characters selected by Magretti are not constant enough for the separation of the two species, and we have thus been compelled to sink the former species under the latter.⁸

In.18229. A well-preserved *T. (H.) gribodoi* with a detached head of the same species. The colour of the insect has been somewhat intensified by the copal and part of the ventral surface of the thorax, abdomen and legs appear whitish. This is probably because of air bubbles under the chitin of the insect.

In.18214. At first glance the insect in this piece of copal appears different from the other specimens mentioned above, owing particularly to the yellow-brown abdomen, ruby eyes and the reddish-tinted cloud on the apical region of the forewings. This intensified colour, however, appears to be some effect of the copal.

In.18220. Two *T. (H.) gribodoi*, and additionally two well-preserved detached legs almost certainly belonging to the same species. One of the two insects is well preserved but the upper portion of the head and thorax has been pared away during the polishing of the copal and it is surrounded by cracks. The second insect is also well preserved but again has a distinct reddish tinge, particularly noticeable in the eyes.

In.18226. A single *T. (H.) gribodoi*, fairly well preserved but with the head partly pared away. Thorax and legs show many white 'air-bubbles'. On the abdomen the pale bands indicate exposure of the thin intersegmental membrane as a result of distension of the abdomen.

58622. A single specimen surrounded by fairly copious air-bubbles in the copal. However, from the side, the specimen is relatively clear to view and is seen to belong to *T. (H.) gribodoi*. A white rim to the eye and the white sheen to the wings are

⁸ The characters chosen by Magretti (1895 : 157) to separate *T. bottegoi* from *T. gribodoi* were: 'per la superficie minutissimamente punteggiata, quasi liscia e nettamente splendente del capo, del mesonoto e dello scudetto; per presentare l'area dell'ocello mediano e la linea mediana frontale leggermente distinte ed infine per la colorazione giallo-testacea dello scapo antennale, delle mandibole, del labro et delle due paia di zampe anteriori.' [. . . in having the surface very finely punctured, being almost smooth and distinctly shiny on head, mesonotum and scutellum; in showing the area of the median ocellus and the median frontal line faintly distinct and finally by the yellow-testaceous colour of the antennal scape, of the mandibles, labrum and the two anterior pairs of legs.]

believed to be spurious effects. It is slightly larger than the others, but the size of worker bees often varies considerably.

Subgenus *TETRAGONA* Lepeletier & Serville 1828

*1828 *Tetragona* Lepeletier & Serville : 710.

GENOTYPE. *Trigona elongata* Lepeletier & Serville 1828 (= *Centris clavipes* Fabricius 1804).

DIAGNOSIS. The inner face of the hind tibiae unevenly gabled but with a sharply elevated, median, plateau-like area that extends from the base almost to the apex and contrasts strongly with a wide, flat, posterior rim (particularly widened at the apex); the contour of the hind tibiae more or less clavate, with the apex in all cases much wider than the base and sometimes conspicuously expanded; plumose hairs in addition to simple hairs usually present along the posterior lateral contour of the hind tibiae or present over their outer face near the base, or both.

REMARKS. The above is *verbatim* from Schwarz (1948).

Trigona (Tetragona) succini (Tosi 1896)

*1896 *Meliponorytes succini* Tosi : 352, pl. 6, figs 1-8.

1907 *Meliponorytes succini* Tosi ; Handlirsch : 892.

1909d *Meliponorytes succini* Tosi ; Cockerell : 5.

1925 *Meliponorytes succini* Tosi ; Schröder : 254.

1928 *Meliponorytes succini* Tosi ; Wheeler : 97.

1948 *Meliponorytes succini* Tosi ; Schwarz : 8.

1964 *Meliponorytes succini* Tosi ; Kerr & Maule : 2.

HOLOTYPE AND PARATYPES. Museo di Mineralogia dell'Univ. di Bologna.

DISTRIBUTION. Miocene, Sicilian amber.

DIAGNOSIS. Length 4 mm; head subquadangular, mandibles apparently with only two denticles; inner surface of hind tibia plateau-like, of sharp elevation, with the posterior and apical rim fairly flat and wide; inner face of hind basitarsus contains a smooth, bristleless area; the hairs along the posterior edge of tibia appear to be plumose.

DESCRIPTION. Dark, except abdomen which tends to be reddish. Compound eyes large, oval and naked. Ocelli situated in a slightly curved line, the lateral ones prominent, the median one lying in a furrow. Face slightly convex, pubescent, and the facial area itself ellipsoidal, slightly hairy and prominent. Clypeus almost triangular and provided with hairs. Vertex double-humped, divided by a median sulcus. Antenna twelve-segmented, the scape long, about one-third the length of the antenna, creased at point of insertion. The structure of the antenna is given in some detail by Tosi, but cannot be said to differ materially from the Recent *Tetragona*, unless Tosi's implication of the rather naked first to third flagellar segments is regarded as significant. Labrum extended, 'becoming round and hollowed like a bowl'. Mandibles with two denticles. Tongue hairy with dilated apex. Labial

palps apparently four-segmented with long first segment. Thorax essentially as in Recent *Tetragona*, with long hairs on ridge of scutellum. Tegulae well developed.

Wings hyaline but hairy, not extending much beyond the abdomen which appears to be fully extended (maybe distended). The main features of the forewing are as follows. Stigma very distinct, lanceolate in form; first submarginal cross vein not strong; marginal cell open at its extremity.

An antennal cleaner is present, and its 'auschnitt' lined with hairs. Basitarsus as long as the remaining tarsal joints taken together and covered with setae. Posterior tibia well developed and covered apically with thick, long hairs, but basally with fewer and more robust hairs. Last tarsal joint larger than the others (except the basitarsus) and cylindrical. Pulvillus large.

Abdomen ovoid, segments all the same size with longer hairs along posterior rim. First abdominal segment hollowed anteriorly. Ventral surface hulled and its first segment furnished with rows of longish hairs. A median sulcus follows the shape of the rows.

REMARKS. This species has been placed in the subgenus *Tetragona* not only on general morphology, but particularly on the structure of the hind leg. If Tosi's figures are carefully examined the inner surface of the hind tibia shows both a main ridge and also a clear dark zone posterior to it. This provides reasonable evidence that the inner surface is indeed plateau-like, of sharp elevation, with a flat posterior rim.

Schwarz (1948) who reviewed Tosi's species came to no definite conclusion with regard to them. He did, however, raise some meticulous points, and rightly or wrongly insisted upon very minute and difficult detail. He refers, for instance, to the two denticles on the outer half of the apex of the mandible instead of the inner half. It is true Tosi illustrated them in such a position and number, and this may have been accurate for a Miocene genus, but it must in any case have been an achievement for Tosi to recognize denticles at all. The distinction of inner and outer halves may have been well-nigh impossible. Again the appearance of obliqueness of the lateral ocelli is obviously influenced by the diffraction of light through the uneven amber surface and cannot be given the significance which Schwarz would like to attribute to it. The latter's reference to the length of the wing and to the stigma is non-committal.

Trigona (Tetragona) iridipennis Smith 1854

(Pl. 2, figs 8, 9)

*1854 *Trigona iridipennis* Smith : 413.

1858 *Trigona laeviceps* Smith : 51.

1921 *Meliponorytes* (?) *devictus* Cockerell ; Cockerell : 544, text-fig. 4.

1922 *Trigona laeviceps* Smith ; Cockerell : 714.

1922 *Meliponorytes* (?) *devictus* Cockerell ; Cockerell : 714.

1964 *Trigona (Tetragonula) devictus* Cockerell ; Kerr & Maule : 11.

SPECIMENS STUDIED. British Museum (Natural History), In.20702 (holotype of *Meliponorytes* (?) *devictus* Cockerell) and In.43809 (identified by Cockerell as *Trigona laeviceps* Smith).

FOSSIL DISTRIBUTION. Probably Pleistocene, Burmese amber : Hukong Valley.

DIAGNOSIS. Length 4 mm. Head and thorax black, face with short, silvery pubescence rather variably distributed, labrum and mandibles ferruginous, antennae testaceous, margins of thorax and scutellum fringed with fuscous pubescence and the sides of the metathorax with a silvery pubescence, elsewhere smooth and shiny ; wings subhyaline, iridescent ; abdomen ferruginous or the base testaceous, smooth and shining, extreme apex pale testaceous, ventral surface with short, silvery pubescence ; apical joints of tarsi testaceous.

DESCRIPTION. Cockerell's description of specimen In.20702 apparently reflects the distortion which would be encountered in looking through the spherical bead containing the specimen, but the bead has now been cut and the following details may be regarded as reliable. Length 4 mm. Head and thorax black, the abdomen and mandibles ferruginous, tarsi testaceous. The naked eyes are red but this cannot be considered the natural colour, the head is broad but not unnaturally so, and the ocelli are prominent, in a curve on the vertex, and have also taken on the reddish tinge. The antennae appear normal in position, size and shape for *T. (T.) iridipennis* ; the scape certainly cannot be considered long and the curve is only slight ; the flagellum is thick and short.

The mesothorax is raised and the scutellum projects, but neither of these features is striking. Hairs are not much in evidence but a few can be perceived on the thorax and on the ridge of the scutellum ; this apparent nakedness, however, is what must be expected of white pubescence on fossilization in amber.

Femora not especially robust, hind tibiae broadened at apex, triangular rather than clavate. Hind basitarsi are at most only half the length of the tibiae and cannot be described as large ; on the other hand, the abdomen is not short for the size of the creature. Forewings subhyaline with a well-developed pale stigma, but folded over the body so that the venation cannot be determined, except that the junction of the basal nerve and cross vein cu-a is coincident. Claws simple, pulvilli large.

The specimen In.43809 was referred by Cockerell to the Recent *Trigona laeviceps* Smith, which is synonymous with *T. (Tetragona) iridipennis* Smith.

REMARKS. Although the specimens look different, when examined superficially, the abdomen of '*M. devictus*' being long and that of '*T. laeviceps*' short, broad and curved downwards, they are conspecific since the differences in the abdomen are due to accidents of fossilization, the first being inflated by gases of putrefaction, the other strongly constricted, as if dried.

'*T. laeviceps*' Smith had already been synonymized with *T. iridipennis* Smith by Schwarz (1948). On the other hand, the comparison of *M. devictus* with Recent species has led us to its identification with *T. (T.) iridipennis*. Cockerell, therefore, was mistaken in assigning these two specimens to two different genera and species.

The reasons for Cockerell's mistake are interesting. In 1921 when Cockerell investigated the first piece of amber, he was under the impression that it was of Miocene age and in consequence placed his specimen under a Miocene genus, *Meliponorytes*. It was in the following year that he received a communication to

the effect that this amber was, in fact, very much more recent. Consequently the specimen described in that year was referred to the modern *Trigona laeviceps* Smith which, as we have seen above, is a synonym of *T. (Tetragona) iridipennis* Smith. Unfortunately Cockerell never rechecked the specimen he designated as *Meliponorytes (?) devictus* and in consequence the latter name has persisted in the literature until now.

Subgenus indet.

Trigona sicula (Tosi 1896)

- *1896 *Meliponorytes sicula* Tosi : 355, fig. 9.
 1928 *Meliponorytes sicula* Tosi ; Wheeler : 97.
 1948 *Meliponorytes sicula* Tosi ; Schwarz : 9.

HOLOTYPE AND PARATYPES. Museo di Mineralogia dell'Univ. di Bologna.

DISTRIBUTION. Miocene : Sicilian amber.

DIAGNOSIS. Three times larger than *T. (Tetragona) succini*, i.e. about 12 mm long ; mesonotum a little less arc-shaped, hind basitarsus narrower and longer. Mandibles with two terminal notches ; pterostigma wanting.

DESCRIPTION. The following characters are common with those of *T. (Tetragona) succini* : (1) large oval eyes, (2) situation of ocelli, (3) antennae, (4) labial palps, (5) claws and pulvillus, (6) hairy tongue, (7) prominent scutellum with long hair. The species appears to have been rather dark in coloration and the wing very similar to that of *T. (T.) succini* except for the lack of stigma.

REMARKS. The subgenus unfortunately cannot be determined. The specimens themselves are sufficiently like *succini* to be considered to belong to *Trigona*, although they lack the stigma, but their large size is a little perplexing. Again, the specimens are not well preserved, and in consequence inadequately described. Tosi wondered whether the species was not a *Melipona*, but in view of the present limited distribution of the latter in South America, and the prevalent ideas of the phylogeny of this group, the latter suggestion is not a happy one. Only a re-examination of the type may shed light on the problem. The diagnosis given above is of necessity comparative, in view of Tosi's manner of description. Yet it must be remembered that the stigma illustrated by Tosi is much as in some *Tetragona*. Again, the comb and pollen rake of the hind tibia are notoriously difficult to detect in some fossil forms and are poorly developed in some Recent members of *Tetragona*. Failure to detect them, therefore, may be taken as an indication of their smallness, not of their absence.

The decision to include the present specimens in *Tetragona* was mainly the result of a study of their leg contours, as already mentioned. The wing venation, however, caused difficulty. According to Tosi vein Cu_2 is redundant and vein Cu_1 meets vein A at the distal and lower apex of cell 2nd Cu . Nevertheless, a slight furrow, which appears to exist in this vicinity in Recent forms, could, if it existed in fossil forms, have given rise to the latter illusion. Again, since the junction of the veins

Cu₁, A and Cu is unknown in Apidae, it is fairly obvious that a mistake has been made here. With regard to cross vein cu-a, not only does it lie along a rather abnormal slope but its relation to the basal vein is peculiar. Possibly in his figure Tosi has rather unwittingly exaggerated the junctions of the veins in this region in an effort to clarify their course.

More than eight specimens of these fossil bees were found in one piece of amber.

Tribe **APINI** Latreille 1802

DESCRIPTION. This Old World tribe is unique among bees in the form of the male genitalia which, unfortunately, are as a rule not accessible in fossil forms.

The Apini have the following characters in common with the Meliponini: scutellum raised, malar space short, ninth sternum modified. Forewing with first recurrent vein angulate or curved. Hindwing with jugal and anal lobes.

The following features are diagnostic for Apini. Eyes densely hairy in Recent forms. Sting well developed. Either one outer tibial spur on hind leg or none; hind basitarsus usually broad as tibia and always rectangular, with a depstum, or the latter broadened into an auricle; basitarsal brush without the small bristleless or differentiated area; claws cleft.

Wings never extending much beyond the body. Distal cells of forewing always complete, marginal cell parallel-sided for a large part of its length in Recent species, but not parallel-sided and smaller and deeper in early fossil forms; pterostigma becoming reduced, not tapering beyond base of vein r.

REMARKS. Most of the known fossil Apidae belong to this tribe, the most important and interesting of all as it embraces the honey bee *Apis mellifera* (p. 249). As a result, the evolution of this remarkable insect can be reconstructed in a detailed manner.

Genus **ELECTRAPIS** Cockerell 1908

*1908b *Electrapis* Cockerell: 326.

1909d *Electrapis* Cockerell; Cockerell: 7.

GENOTYPE. *Apis meliponoides* Buttel-Reepen 1906, by monotypy (Cockerell 1908).

DIAGNOSIS. Body morphology not very bomboid (p. 157) but wing venation retaining bomboid characters. Either a single outer hind tibial spur or none. While the body may have a variable quantity of hair, that on the eyes is scant or non-existent.

DESCRIPTION. Variable in size and shape; from 4 mm to 14 mm in length. Normal disposition of tip of abdomen slightly ventral and proximal.

Head. Moderately large and somewhat square; tuft of hair on the vertex often present; compound eyes moderately convex and ocelli prominent. Male has eyes far apart and the facial quadrangle is squarish.

Mouth parts are well known only from Cockerell's descriptions, which may not apply to all species. They are as follows. 'Mandibles truncate, much as in *Apis*, but the cutting edge with two notches; labrum semicircular, tongue elongate and both it and the labial palpi essentially as in *Apis*; spoon on end of tongue small, maxillary palpi very small, thick, apparently 2-jointed, malar space very short; anterior end of clypeus straight'. The little that can be discerned in *E. apoides* Manning, however, suggests a single notch in the cutting edge of the mandibles, and an elongate 'tongue' with a rather large flabellum.

Antennae moderately long, sockets large; scape relatively long and curved, usually broadened distally and often articulating with a 'knob-shaped' pedicel or first joint of the flagellum. Male antennae longer than female.

Thorax variable; (1) long and broad in proportion to the size of the insect, tapering sharply distally, very reminiscent of some *Trigona*; (2) less broad and more slender, proportionately more reminiscent of *Apis*; (3) more spherical in shape, usually well covered with hair, somewhat reminiscent of *Bombus*. Scutellum always distinct and often prominent.

Front leg. Antenna cleaner always present but structurally slightly different from Recent *Apis*.

Middle leg. Outer surface of tibia well provided with stout hairs. A single spur present at apex of tibia, stouter than that of hind leg. Basitarsus with long strong hairs.

Hind leg. Tibia much longer than basitarsus. Posterior fringe of hairs on the tibia well developed and believed to contain some plumose hairs among the simple ones. Corbicula and pollen rake present. Sometimes a ridge covered with fine hairs occurs on the inner surface of the tibia. Basitarsus rectangular, with a brush and often a small differentiated area.

Claws bifid. **Pulvilli** fairly large.

Abdomen. Usually oval in shape and, at most, only moderately clothed with hair. In *E. (Roussyana) palmnickenensis* the hairiness of the sternites resembles an abdominal brush, usually as broad as the tibia or nearly so. The shape of the abdomen as figured by Buttell-Reepen (1906) may not be typical of the whole genus; another known type has one edge convex, more like that of a recent *Apis* worker. The 'auschnitt' of the auricle between tibia and tarsus is deep and well formed, but there is only an incipient development of the depstum. A single outer spur is typically present.

Forewing. Pterostigma variable in size and shape. Marginal cell moderately long and generally broader than that of Recent *Apis*, ending away from wing margin in a stub. Vein second r-m always curved, mostly S-shaped, but much more upright than in Recent *Apis* and meeting M very slightly distad of the junction of M and second m-cu; first r-m at right angles to M; base veins of cells first R₁ and first Rs form a Y with first submarginal cross vein; the junction of first m-cu with M is angular as described, but not illustrated, by Cockerell (1909d). This junction is beyond half the wing length and thus much more distal than in Recent *Apis*.

The basal vein meets at the base or just proximad of stigma and is gently S-shaped. It runs into Cu slightly proximad of the junction of the latter with cross vein cu-a, or the junctions here coincide. Lower section of basal vein (M) not less than twice the length of the upper section of basal vein (Rs). Vein Cu₂ is fairly short.

Hindwing. Hamuli variable (6-16, cf. *Chalcobombus* with 8-11). Cross vein cu-a oblique, the slope being posterior and basad, as in Recent *Bombus* and opposite in direction to that of Recent *Apis*; M runs almost to wing margin; cross vein r-m well defined, but only at most, slightly oblique, while Rs, like M, almost reaches wing margin. The general shape is more elongate than Recent *Apis*, and the wing possesses distinct and well-characterized anal and jugal lobes.

Wings, in general, hyaline, fuliginous or fuscous and of moderate size, rarely longer than the body length though from their point of insertion on the thorax they often extend beyond the abdomen. Sometimes a fairly large, dark-coloured cloud (about one-twelfth total area) is present in the forewing. Most wings are hairy, but there is some doubt as to whether this applies to all species.

REMARKS. Most authors have held *Electrapis* to be directly ancestral to Recent *Apis*. This view is likely to be correct regarding only *Electrapis* s. str., here treated as a subgenus. The other species show clear signs of deviation. On the whole, however, one cannot separate these groups as distinct genera, as too many characters overlap. It is in fact impossible to give clear diagnoses of subgenera, and the three subgenera here distinguished are to that extent arbitrary. They are:

- (1) a group with *Apis*-like characters: *Electrapis* Cockerell 1909d, s. str.;
- (2) a group with *Bombus*-like body and *Apis*-like venation; *Protobombus* Cockerell 1908b;
- (3) a *Trigona*-like group: *Roussyana* Manning 1960.

Cockerell (1909d) and Zeuner (1944, 1951) considered that the species of *Electrapis* were social insects. As evidence Cockerell pointed out the occurrence of many specimens crowded together in a small piece of amber (*E. meliponoides*), whilst Zeuner considered the structure of the collecting apparatus. On other grounds too, this contention can be supported. [See also Appendix, p. 257.]

Subgenus *ELECTRAPIS* Cockerell 1908

- *1908b *Electrapis* Cockerell : 326.
1909d *Electrapis* Cockerell ; Cockerell : 7.

GENOTYPE. *Apis meliponoides* Buttel-Reepen 1906, by monotypy (Cockerell 1908b).

Electrapis (Electrapis) apoides Manning 1960

- *1960 *Electrapis (Electrapis) apoides* Manning : 306, pl. 5, fig. 1.
1970a *Electrapis apoides* Manning ; Kelner-Pillault : 16, pl. 2, figs 1, 2, text-fig. 5A.

HOLOTYPE. No. 94 in the Bursey Collection (see p. 159), now in the Muséum National d'Histoire Naturelle, Paris.

DISTRIBUTION. Eocene, Baltic amber.

DIAGNOSIS. Body 6.5 mm long, hairy. Forewing 6 mm. Hind tibia comparatively short and stout, with a single, much reduced, spur; corbicula exceptionally well developed with strong curved hairs on the posterior edge; basitarsus square and flat, but with the posterior edge markedly convex. Wings fuliginous with a cloud apically; pterostigma large; eight hamuli.

DESCRIPTION. Specimen well preserved, blackish. Total length 6.5 mm; thorax 2.75 mm long and 2.25 mm wide; abdomen 2.75 mm long and 2.5 mm wide; forewing 6 mm; hind tibia 2.75 mm.

Proboscis extended for approximately the length of the head, provided with a large flagellum. Antennae very much like those of *E. (Roussyana) proava* (p. 236), with a similarly shaped, knob-like pedicel.

The forelegs differ from those of other species of *Electrapis* in the shape of the antenna-cleaner. The zone of articulation between tibia and tarsus is greatly reduced, and the latter limbs are rounded, and not square, at their point of insertion. The clasp, too, is more highly developed, now having a fully shaped lobe and a distal tip projecting over and against the distal edge of the notch. The middle legs cannot be studied in detail, since they lie too much under the body of the insect. They are, however, well provided with hairs and appear to possess a single strong spur.

The hind legs are well proportioned, and not lanky as in *E. (Roussyana) proava*, and the hairs of the posterior margin of the corbicula are possibly plumose. On the apical margin of the tibia, posteriorly, a fine-haired rake is present, and the 'auschnitt' of the auricle is well developed. Moreover, the internal spur on the hind tibia is present and visible on the left leg of the specimen as viewed from behind. It is thicker and about one and a half times as long as the hairs of the anterior edge of the leg, but it is evidently in a state of reduction, being so small as hardly to serve any useful purpose. The basitarsus, although squarish, is elegantly shaped, with graceful curved outline, and not coarsely square as illustrated by Cockerell for *Chalcobombus*. Its inner surface is equipped with strong, almost bristle-like, hairs, which are arranged in rows as can be seen for those situated at the distal extremity.

The wing venation does not differ materially from that of *E. (R.) proava*. Possibly the basal nerve of the forewing is slightly less curved, and the radius stronger. The hindwing is preserved in its entirety and exhibits eight hamuli, and well-developed jugal and anal lobes. Only one anal vein is known to be present, but the two lobes are separated by a deep cleft. A line that could be regarded as 4H is probably no more than a fault in the amber. Veins Rs and M continue almost to the wing margin, cross vein r-m slopes basad posteriorly, and cross vein cu-a exhibits a similar, but more oblique, slope.

On the whole, the creature itself has the habitus of a small *Apis*. The head is well proportioned and neatly tapering, less square than some other species of *Electrapis*, and the thorax has neither excessive width nor length. The abdomen, however, is still rather small, though the habit of holding the tip ventrally, together with the presence of an air bubble on this particular specimen, rather prevents

accurate observation of this point. The wings still project some distance beyond the apex of the abdomen.

REMARKS. The specimen was kindly lent by the late Mr Bursey of Surbiton, Surrey, to whom we acknowledge our thanks.

Electrapis (Electrapis) meliponoides (Buttel-Reepen 1906)

(Pl. 3, figs 5, 6)

- *1906 *Apis meliponoides* Buttel-Reepen : 158.
 1907 *Apis meliponoides* Buttel-Reepen ; Handlirsch : 892.
 1908b *Electrapis meliponoides* (Buttel-Reepen) ; Cockerell : 326.
 1909d *Electrapis meliponoides* (Buttel-Reepen) ; Cockerell : fig. 4.
 1915 *Apis meliponoides* Buttel-Reepen ; Buttel-Reepen : 10, fig. 3.
 1915 *Electrapis meliponoides* Butt.-Reep. ; Buttel-Reepen : 12.
 1928 *Apis meliponoides* Buttel-Reepen ; Wheeler : 98.
 1928 *Electrapis meliponoides* (Buttel-Reepen) ; Wheeler : 98.
 1931 *Apis meliponoides* Buttel-Reepen ; Statz : 40.
 1931 *Electrapis meliponoides* Butt.-Reep. ; Statz : 41, figs 2, 3.

HOLOTYPE AND PARATYPE. Two specimens in the Westpreussisches Provinzial-Museum, Danzig.

MATERIAL. Cockerell's specimens (1 male, 7 females), Koenigsberg Collection. Also Nos. 238 and 461 in Scheele Collection, Geologisches Staatsinstitut, Hamburg. No. 238 is also Typen-Katalog des Geol. Staatsinstitut, No. 149.

DISTRIBUTION. Eocene, Baltic amber.

DIAGNOSIS. Body 14 mm. Body hairy but scant hair on eyes ; basitarsus comparatively long, broad and flat, posterior edge not convex ; wings fuliginous.

DESCRIPTION. Cockerell's description can be summarized as follows (the measurements quoted in hundredths of a millimetre by Cockerell are to a degree of precision as unnecessary as it is misleading). Black, much erect fuscous hair on head and thorax. Tibia and tarsus with coarse fuliginous hair ; wing venation remarkable only for the small, piceous, stigma ; it is thought, too, that the upper section of the basal vein is comparatively short. Male specimen with eyes far apart ; facial quadrangle square ; antennae long, over 5 mm with last joint obliquely truncate.

The following description is based on specimen No. 238 (Scheele Collection), which one of us (F. J. M.) was able to study in Hamburg. At first sight the fossil appears to be poorly preserved, in fact so much is covered with 'schimmel' that only a few segments of the abdomen can be discerned. The left forewing and hindwing, however, are both completely intact and the right forewing also shows much of the venation. Moreover, many parts of the legs are preserved, as well as the sting, and the hairiness of the thorax and the colour of the abdomen are clearly perceptible. Unfortunately, the head is completely missing.

The specimen has the following measurements : overall length, without head, 12 mm ; length of forewing, 9.5 mm ; hindwing 6 mm ; basitarsus 2.25 mm.

The copious hairs on the thorax are erect and fuscous. The abdomen is black, but each segment appears to have a band of dark brown distally ; it is hairy but the

hairs are smaller and darker than those on the thorax. They are, however, longer at the apex of the abdomen. The sting protrudes considerably and is strong and straight. In Recent *Apis* a straight sting is characteristic of the worker, that of the queen being distinctly curved.

The many fragments of legs cannot be entirely pieced together. It is evident, however, that the claws are bifid and the distitarsi cordiform. The tibia, which can easily be recognized as such, has unfortunately had the outer surface pared away during the polishing of the amber. The corbicula, therefore, is lost, but the strong hairs of the anterior edge, which have not been destroyed, give complete proof of its earlier presence, if such were needed. There is no evidence for a tibial spur. This does not imply absence in view of the fragmentary character of the legs. The basitarsus is large, broad and flat, three-quarters the length of the tibia, the posterior edge quite straight and the posterior distal angle quite acute. Unfortunately the details of the structure at the junction of the basitarsus with the tibia are mostly masked by decayed pollen so that the depstum is not known. The strong non-plumose hairs of the anterior apex of the tibia, however, are present exactly as in Recent *Apis* and there is reason to suspect that the pollen rake has strong teeth. There is no evidence whatever for the presence of a pollen comb, but the pollen brush of the basitarsus is present. The strong hairs are arranged in rows with pollen still adhering to them. Approximately 17 hairs comprise the bottom row.

The hairy forewing has a large cloud, and is slightly papillate apically. The wing venation is that of *Electrapis* but a slight elongation of the wing itself has brought about a few minor modifications. These are a narrowing of the apex of the marginal cell, an elongation of the third submarginal cell and the second M. Proximally there is an increase in the length of the basal nerve with a consequent compensating alteration on the shapes of the first submarginal cell and the first M. The junction of basal nerve and cross vein cu-a is coincident on Cu, and vein cu-a slopes slightly apicad. Pterostigma piceous, but not small, though rather weak.

The hindwing is particularly interesting because of the increase of the number of hamuli to 16.

The other specimen from the Scheele Collection (No. 461) is poorly preserved, and covered with much 'schimmel'. Only part of a hindwing is well preserved. The insect is reminiscent of specimen No. 238, agreeing with it in all available characters. Length, with head, at least 13 mm; hind basitarsus rectangular and long, almost as broad as tibia, and with a straight posterior edge; hindwing in venation and shape agreeing with No. 238 except that the base is slightly shorter and the lobes deeper, and cross vein r-m appears more oblique. These characters can be accounted for by the oblique angle at which the wing must be viewed through the amber. At least 16 hamuli are present.

The remaining features are taxonomically unimportant. They include the presence of two well-developed antennae inserted on the lower half of the face; thorax possibly well supplied with hairs; wings extending to tip of abdomen and probably beyond; and the presence of legs whose broad outlines only can be ascertained.

REMARKS. Cockerell defined the hind basitarsus of his specimens as 'broad and flat, as figured by Buttel-Reepen (*Apis meliponoides*)'. His specimens are thus considered to be identifiable with the latter.

Buttel-Reepen was rather obsessed with the idea that *E. meliponoides* was intermediate in character between Recent stingless bees and Recent honey bees. What is probably true is that both groups evolved from some common ancestral form and that the Eocene *E. meliponoides* represents one member of this evolving series. Moreover, Buttel-Reepen stressed his point exclusively with regard to the hind basitarsus, which alone he described. From the descriptions here given, however, it is clear that the basitarsus has little that can be described as typically meliponid.

Electrapis (Electrapis) tornquisti Cockerell 1908

- *1908b *Electrapis* (?) *tornquisti* Cockerell : 326.
 1909f *Electrapis* (?) *tornquisti* Cockerell ; Cockerell : 23.
 1928 *Electrapis tornquisti* Cockerell ; Wheeler : 98.
 1931 *Electrapis* (?) *tornquisti* Cockerell ; Statz : 41.
 1931 *Electrapis tornquisti* Cockerell ; Salt : 145.

HOLOTYPE. Geological Museum, University of Königsberg.

DISTRIBUTION. Eocene, Baltic amber.

DIAGNOSIS. Length of body 11.5–12 mm ; robust and more *Bombus*-like than the previous species ; head and thorax abundantly hairy, but face with scant hair ; fourth antennal joint conspicuously shorter than fifth ; wing hyaline, stigma almost lacking ; hindwings with 15 hamuli ; abdomen broad.

DESCRIPTION. A hairy bee, more so than *E. (E.) meliponoides*. Coloration of thorax anomalous. The broad abdomen, although apparently black, has the hind margins of the segments rather broadly seamed with white. Pubescence of abdomen short and pale. Tegulae large with very fine delicately plumose hairs.

Venation differing from *E. (E.) meliponoides* in the rather distal position of the cross vein cu-a which lies slightly distad of the junction of the basal vein with Cu. It further differs in the lower part of this vein being strongly bent basad. It agrees with it, however, in that section Rs of the marginal cell is concave.

REMARKS. Although this specimen, on general morphology, is more bomboid than other *Electrapis* s. str., it has been retained in this section for convenience. The species was listed with some characters in 1908, but was not fully described until 1909.

Subgenus **PROTOMBOMBUS** Cockerell 1908

- *1908b *Protobombus* Cockerell : 327.
 1909d *Protobombus* Cockerell ; Cockerell : 10.

GENOTYPE. *Protobombus indecisus* Cockerell 1908, by monotypy.

DIAGNOSIS. Wings comparatively apoid, and more bomboid, than in *E. (Electrapis)*.

DESCRIPTION. Body globose, compact and *Bombus*-like. Compared with *E. (Electrapis)* it appears to have a greater range of notches on the mandibles (1-3), the elevation of the scutellum is accentuated and the inner tooth of the claws is shallower. It agrees with *E. (Electrapis)* in size (7-10 mm), in its hairless eyes, comparatively large wings, gently convex posterior margin of the basitarsus, tibial spur of the middle leg, large ocelli and large pulvillus. The hind tibial spur may or may not be present.

Forewing. Stigma almost wanting. Marginal cell longer than in *E. (Electrapis)* but still ending obtusely at a distance from wing margin. All the submarginal cells exhibit peculiarities, in particular the second which is, according to Cockerell, 'very broad, pentagonal, much longer than third on marginal, and receiving 1st recurrent nervure (1st m-cu) at or a little beyond end of its first third'. The latter feature is remarkable in that it shows a definite advance towards the *Synapis* wing. This point, however, is further emphasized by the first and second submarginal cross veins being 'equally oblique in opposite directions', and also by the fact that the third submarginal cell is produced apically, by implication presumably more so than in the *E. (Electrapis)* wing. In these points the wing is markedly apoid. It is not a *Synapis* wing, however, since the base of the third submarginal cell receives the second m-cu vein one-sixth from its end, and the first m-cu has a bend or angle in its upper part. Such characteristics are typical of the genus *Electrapis* as are also the remaining characters quoted by Cockerell.

Hindwing. Vein cu-a strongly oblique with sometimes a slight double curve.

REMARKS. Cockerell considered this genus to be ancestral to *Bombus*. This point of view, however, is difficult to maintain since *Protobombus* has a more apoid wing than even *E. (Electrapis)*, though its body is somewhat reminiscent of *Bombus*. The wide divergence from *Bombus* may be more easily appreciated if the evolutionary sequence of the second submarginal cell, in relation to the position at which it receives the first m-cu vein, is summarized:

Chalcobombus - beyond (distal of) the middle.

Electrapis (Electrapis) - just beyond or at the middle.

Electrapis (Protobombus) - much [Cockerell's term] before the middle.

Synapis - about one-third before middle.

Apis - about one-quarter before middle.

Electrapis (Protobombus) indecisus (Cockerell 1908)

*1908b *Protobombus indecisus* Cockerell : 326.

1909d *Protobombus indecisus* Cockerell ; Cockerell : 10, fig. 5.

1931 *Protobombus indecisus* Cockerell ; Salt : 146.

HOLOTYPE. Geological Museum, University of Koenigsberg.

DISTRIBUTION. Eocene, Baltic amber.

DIAGNOSIS. About 10 mm long ; mandibles obliquely truncate with three notches on cutting edge ; basitarsus broad.

DESCRIPTION. A blackish bee, but base of abdomen brownish, with sparse pale hair. Thorax and occiput densely covered with rather short, plumose, whitish hair. Legs and tegulae on the whole blackish with pale hair. The distinctive feature of the pale fuliginous wing is a dark cloud at end of marginal cell.

REMARKS. Listed by Cockerell with a few characters in 1908, but not fully described until 1909.

Electrapis (Protobombus) tristellus (Cockerell 1909)

*1909f *Protobombus tristellus* Cockerell : 24.

1931 *Protobombus tristellus* Cockerell ; Salt : 146.

HOLOTYPE. Geological Museum, University of Koenigsberg.

DISTRIBUTION. Eocene, Baltic amber.

DIAGNOSIS. About 7 mm long ; much erect hair on vertex ; wings approximately 6.7 mm long ; abdominal segments black with hind margins 'rather broadly pale reddish' ; anterior margin of basitarsus gently convex ; glossa, as preserved, short ; mandibles long, falciform with a single deep notch ; last two joints of labial palpi rather large ; eyes wide apart above.

DESCRIPTION. A blackish bee ; mesothorax and scutellum as well as vertex with much erect black hair, abdomen as described above. The forewing has a large, conspicuous fuliginous cloud. Venation as in *E. (Protobombus) indecicus*, except for a presumed double curve of the long, oblique vein cu-a of hindwing. Mouth parts appear to be well preserved and differ in several respects from those of *E. (Electrapis) meliponoides*, for instance in the short broad glossa and the large flabellum. The length of the mouth parts, however, is difficult to ascertain in fossil forms, since they may not be completely extruded. Little reliance, therefore, should be placed on this character for diagnostic purposes.

REMARKS. This specimen was not listed by Cockerell in 1908.

Subgenus **ROUSSYANA** Manning 1960

GENOTYPE. *Apis palmnickenensis* Roussy 1927, by original designation.

DIAGNOSIS. This subgenus embraces the more *Trigona*-like members of the genus *Electrapis*. These bees exhibit, however, all the characters of this genus, in so far as they are known. They are distinguished by the habitus of the body which is reminiscent of the stingless bees.

Electrapis (Roussyana) palmnickenensis (Roussy 1937)

(Pl. 3, figs 1, 2)

*1937 *Apis palmnickenensis* Roussy : 66, fig. 13.

1938 *Apis palmnickenensis* Roussy ; Armbruster : 89.

1960 *Electrapis (Roussyana) palmnickenensis* (Roussy) ; Manning : 306.

HOLOTYPE AND PARATYPES. Roussy Collection, Aigle, Switzerland.

MATERIAL. In addition to the types, one specimen in Geologisches Staatsinstitut Hamburg (Scheele Collection, No. 218; also listed in Typen-Katalog des Geol. Staatsinstitut, No. 150).

DISTRIBUTION. Eocene, Baltic amber.

DIAGNOSIS. Small, black insects about 4 mm long; scutellum very hairy; sternites with rows of hairs. Inner surface of tibia with a ridge of short hairs covering about a quarter of the posterior surface. Basitarsus less than half the length of, and narrower than, the tibia, its posterior upper apex exhibiting an area clear of bristles and an incipient depstum.

DESCRIPTION. We have inspected M. Roussy's piece of amber containing eight specimens, two of which are complete. The following is the condition of the individual specimens, their numbers agreeing with the semicircular alignment from the left upper corner of the piece of amber towards the right lower corner.

1. Badly preserved, except fore and hind legs. Wing venation masked by 'schimmel'. Possibly not more than 3.5 mm long.
- 2 and 3. Very much alike and well preserved; 3-4 mm long. Details of almost all appendages can be discerned including mandible and proboscis of No. 3. Spur on hind legs distinct. Wings of No. 2 not clear.
4. The best preserved specimen, but parts of some legs cut off. A considerable amount of wing venation can be discerned. 3.5 mm long.
5. Much covered by 'schimmel' but much of the wing venation recognizable. Antennae prominent.
6. Badly preserved and consists only of remains of thorax and legs.
7. Somewhat covered with 'schimmel' and wings cut off short. Insect bent on itself. One antenna present and well preserved.
8. Remains of a head with mandible.

The wings extend well beyond the apex of the abdomen; the head is broad, but less so than the thorax. The antennae are inserted on the lower part of the face and consist of a comparatively long, slightly curved scape and 11 segments to the flagellum; the pedicel appears to be knob-shaped. The eyes are prominent on the side of the head, and the ocelli distinct. The thorax is strong and carries a prominent scutellum. The abdomen is short and oval. The forelegs exhibit a well-developed antenna cleaner with broad flap and deeply rounded 'auschnitt', whilst the hind leg is characterized by a distinct corbicula with scopa, strong pollen rake, and short outer tibial spur but no pollen comb. The basitarsus is rectangular and equipped with a hairy pollen brush on the inside.

In addition to the eight specimens of M. Roussy, another has been found. It is preserved in the Scheele Collection, Hamburg. Through the kindness of Professor E. Voigt and Dr Walter Häntzschel it was lent to us for detailed inspection. Since the piece of amber contains one complete insect, perfectly preserved, and two fragments of legs, one in excellent condition showing tibia and tarsi, it has been possible to obtain a reasonably complete description of it, and the following is based on this specimen.

Size. From head to tip of wing 4.25 mm. Length of forewing 3.25 mm, extending 1.25 mm beyond the tip of the abdomen. Length of hind tibia and tarsus 2 mm. This specimen appears to be longer than the Roussy specimens, but this is deceptive. Though the wings extend conspicuously beyond the abdomen, the length of the body (which cannot be measured accurately) is possibly no more than 3 mm.

Colour. Very dark brown, or blackish. A creamy shading on the notum may be due to the natural colour of its copious hairs, or else it is due to the presence of some pollen.

Head moderately large, black, face sparsely hairy, with cream-coloured pubescence on the vertex. There is a reddish patch around the right ocellus, but this is almost certainly the result of *post mortem* alteration.

The compound eyes are hairless and prominent, and almost reach the bases of the mandibles, so that the malar spaces are much reduced. The three ocelli are large, set on the vertex and arranged in a shallow triangle. The single median frontal suture runs from the middle ocellus downwards.

The clypeus is trapezoid, tapering dorsally because of the convergent slope of the lateral epistomal sutures, and it is not protruding. The mandibles appear to have at least a convex cutting edge. The anterior part of the face terminates in a narrow labrum.

The antennae are not more than moderately long, inserted close together immediately above the frontoclypeal suture and apparently yellow and black. The scape has slightly less than half the length of the flagellum. The flagellum consists of eleven segments mostly subequal in size, though the terminal segment is longer, and those near the pedicel thinner and more tapering, and also darker in colour.

Thorax. Well developed; pronotum short; scutellum very prominent. The whole thorax copiously covered with hairs which are longest on the scutellum, but shorter on the pronotum. Tegulae large.

Abdomen. Small, oval. Tergites not noticeably hairy, though the sternites have rows of well-defined hairs. No intersegmental membranes can be discerned and this is taken as evidence of the rather contracted nature of the abdomen.

Wings. Hairy and fuscous; pattern of wing venation as in *Electrapis*, with the following points of interest; in the forewing the pterostigma is large and deep; the anterior vein bounding the marginal cell, i.e. radius, is not coincident with the wing margin and its course continues beyond the apex of the marginal cell towards the wing apex; cross vein cu-a lies distad of junction of basal nerve with Cu; the hindwing has only six hamuli and both jugal and anal lobes are well developed.

Three anal veins are present in the hindwing. They can be seen if the left hindwing is viewed head-on, i.e. as inspecting the face of the insect.

Legs. Antenna cleaner present on foreleg, 'auschnitt' large, but since the legs are flexed on themselves other structures cannot be clearly identified; middle leg has tibia at least as long as femur, broadening towards apex, and covered with strong hairs, particularly posteriorly. Pollen is entrapped in these hairs. A distinct tibial spur can be recognized on this leg.

The hind leg appears to have a comparatively large trochanter distinctly tapering towards the base; tibia longer than femur, triangular in shape, and with a well-developed scopa; hairs appear somewhat plumose; corbicula moderately well developed, smooth, with few hairs within the corbicula itself; inner surface of tibia with the ridge of short hairs occupying such a position posteriorly that the rim which separates it from the posterior edge of the corbicula is very narrow but the anterior rim is wide. The tibial appendages consist of a small, outer tibial spur, straight, and non-serrate, and a strong pollen rake projecting on a shelf from the inner apex of the tibia; no pollen comb is present, but at the posterior apex of the tibia an angle suggests an incipient auricle. The tibia is not strongly curved, even posteriorly, but the isolated hind leg, because of the curve of the amber, deceptively gives this impression.

The basitarsus is narrower than the tibia and rectangular. The two posterior apices are strongly acute; the inner surface consists of a brush of strong hairs, whose disposition in rows is rather masked by the comparatively great length of the bristles; possibly five rows is the maximum, though the bristles per row cannot be computed; the 'clear' area is present around the posterior upper apex. Distitarsi cordiform.

The claws appear entire at first sight but close inspection reveals a single tooth at about half-way down. Pulvillus well developed.

REMARKS. In 1938 Armbruster criticized Roussy's description of these insects, which admittedly was in a popular style. He failed, however, to appreciate their significance since he was unacquainted with the *Trigona*-like group of *Electrapis*. The very detailed description here given will, it is hoped, fill an awkward gap and establish this group as a natural division of the primitive honey bees. (See also p. 254.)

Electrapis (Roussyana) proava (Menge 1856)

(Pl. 3, figs 3, 4)

- *1856 *Apis proava* Menge : 26.
 1891 *Apis proava* Menge ; Scudder : 689 (5938).
 1907 *Apis proava* Menge ; Handlirsch : 892.
 1909d *Apis proava* Menge ; Cockerell : 7.
 1915 *Apis proava* Menge ; Buttel-Reepen : 10.
 1928 *Apis proava* Menge ; Wheeler : 98.
 1931 *Apis proava* Menge ; Statz : 40.
 1931 *Apis proava* Menge ; Salt : 143.

LECTOTYPE. British Museum (Natural History), In.43592, herein selected.

PARALECTOTYPE. British Museum (Natural History), In.18757.

DISTRIBUTION. Eocene, Baltic amber.

DIAGNOSIS. Body about 6 mm long (after some allowance has been made for a contracted and bent abdomen), length of forewing 6.5 mm. Scant hair on body as well as on eyes; hind leg rather lanky, due to a proportionately long tibia, basitarsus broad, flat and rectangular, posterior edge convex; wings hyaline, almost hairless.

DESCRIPTION. The lectotype, on which the following description is based, is well preserved, blackish in colour, with the terminal portion of thorax becoming paler, the whole body being very scantily supplied with hairs. The actual length of the body is 6 mm, length of abdomen approx. 2.25 mm, width of abdomen 2.25 mm; length of thorax approx. 2.75 mm, width of thorax 2.5 mm; length of hind tibia 3.25 mm.

Head squarish, poorly supplied with hair; ocelli prominent. Mouth parts not known. Antennae as recent *Apis*, but pedicel 'ball-shaped' and scape broadened distally, meeting the pedicel steeply.

Thorax proportionately very broad and thick, tapering sharply distally, not hairy, reminiscent of some species of *Trigona*.

The foreleg has an antenna cleaner of a somewhat primitive type, and well characterized by the clasp, which is long and thin and completely overlaps the hollow. The zone of articulation of tibia and tarsus is greatly extended.

The middle legs have a pronounced spur on the apex of the tibia. This spur is longer and sturdier than the corresponding spur of the hind leg. The outer edge of the tibia is well provided with hairs.

Hind legs fuscous, a little disproportionate on account of the great length of the tibia, the latter provided with long, somewhat plumose, hairs along the posterior edge and a neat row of short hairs down the inner median line. A single spur is present but its position is such that it is difficult to see on the specimen. Basitarsus rectangular, with convex posterior edge, covered with hairs which are strong on the inner side. An auricle is possibly not present but a concavity is present between tibia and basitarsus. One gains the impression that this zone is slightly more primitive than in *Electrapis* (*R.*) *palmnickenensis*. There is a tibial rake, which is stronger and coarser than that of the latter species.

The venation of the forewing is characterized as follows. Stigma comparatively large, vein cu-a at right angles to A and meeting Cu slightly distally of the junction with the basal vein. Upper section of basal vein (Rs) apparently proportionately longer than that of *E. meliponoides*.

Hindwing incompletely preserved. Eight hamuli, compared with six in *E.* (*R.*) *palmnickenensis*. One might be inclined to regard this as a meliponid feature, since *E.* (*E.*) *torquisti* has 15, *E.* (*E.*) *meliponoides* 16 (though *E.* (*E.*) *apoides* has only 8), *Apis* (*Synapis*) *henshawi* has 17, Recent *A. mellifera* 20-23 and *A. dorsata* 23, but the smaller *A. florea* only 12. Recent *Bombus* species have 20-23 and *Euglossa* 27. There appears, however, to exist a relation between the number of hamuli, on the one hand, and body size and power of flight, on the other.

The part of the hindwing which is preserved includes cu-a, r-m and sections of M and Rs, together with cell Cu. It agrees with *E.* (*E.*) *apoides*.

The second specimen, In.18757, is covered with 'schimmel', and is assigned to *E.* (*R.*) *proava* with some reservation. It is larger than the lectotype, being 8.1 mm long. The forewing is 6.8 mm long and shows a dark apical cloud covering about one-twelfth of its area. The venation, in so far as it can be ascertained, appears to be identical with that of the lectotype. We hold that this is Menge's other specimen, as will be shown under 'Remarks'.

REMARKS. It appears that Cockerell (1909d) thought little of Menge's detailed description, and that he never saw the specimens, presumably because he expected them to be in the Koenigsberg Collection.

We have satisfied ourselves that the two specimens, In.43592 and In.18757 of the British Museum (Natural History), are in fact Menge's types, though no specific identification was attached to them. Our reasons are as follows. Two specimens were available to Menge, one almost entire and the other covered with 'schimmel', i.e. with the products of the gases of putrefaction. The first lends itself to description, but the second is in a very poor condition. Menge's description of the first tallies in a remarkable way with the British Museum specimen In.43592, and in a negative manner so does the second, In.18757. Furthermore, the history of the specimens supports this view. They were purchased in 1892 by the Trustees of the British Museum from Messrs Stantien & Becker, first placed in the Zoology Department and later (about 1904) transferred to the Department of Geology (now Palaeontology).

Fossil insects preserved in amber were sold by the above-mentioned firm over a long period of time. Their stocks were eventually taken over by the Prussian State and became the care of the State Amber Collection in Koenigsberg. Before this happened, however, Dr Richard Klebs, a geologist in the Prussian State Geological Survey, was in charge of the amber collection of Messrs Stantien & Becker. A set of 346 specimens were purchased by the British Museum in 1892, which included the two bees in question. These specimens bear labels marked 'R. Klebs, Museum Stantien & Becker'. This suggests that they did not come directly from the amber works of the firm, but were acquired through Dr Klebs. There is other evidence that not only the Menge Collection, but also part of the Germar and Berendt Collections was dispersed with the aid of this firm, and it would appear that Dr Klebs bought up such collections in the first instance and handed them over to the firm at a later date. For this reason specimens of such provenance are usually assigned to the 'Klebs Collection'.

If the specimens In.43592 and In.18757 were obtained by the British Museum in 1892 from Menge's collection *via* Dr Klebs and Messrs Stantien & Becker it is evident that Cockerell could not have found them in the Koenigsberg Collection in 1908.

It now remains to be shown that Menge's descriptions indeed tally with those given here as the result of independent study. Of the well-preserved specimen, Menge says that it is 7 mm long, with the wings 10 mm, breadth 3-4 mm. The abdomen is bent so that the sting lies under the apex of the tarsi of the first pair of legs. The tarsus of the foreleg comprises an antenna cleaner, or rather a sinus ('ausschnitt'). A spur is present on the tibia of the hind leg where it projects from its outer surface, and bristles are present on the digits of the hind feet. The bristles are a little irregularly shaped. The body itself is scantily haired and the ocelli and compound eyes are bare. The latter are oblong and narrow, and separated from each other. Twelve antennal segments are present, and these, together with the shape of the eyes, indicate for Menge a worker bee.

This description is at variance with our observations in two respects. First, the number of segments of the antennae of the fossil cannot be ascertained. Those of

the good specimen (and the other is too obscured by 'schimmel' for any reliable observation) has one flagellum cut off short at the surface of the amber, the other twisted into a difficult position. Menge, however, referred to twelve visible segments for the worker.⁹ The explanation of the discrepancy between descriptions and fossil is believed to be the treatment of the specimen whilst in the hands of Messrs Stantien & Becker. The amber pieces were reduced in size to the minimum, preferably made rectangular, and embedded in a resin in a glass cell on a microscope slide. The polishing process resulted in the loss of the distal portion of the antenna, and parts of the legs. Menge, therefore, may well have been able to study the entire antenna.

The second particular in which the description differs from the fossil is Menge's reference to the abdomen being so bent as to lie under the tarsi of the front pair of legs. The abdomen of the fossil does appear to be bent under the body but certainly not to such a forward position as Menge suggested. Also no sting can be seen. The abdomen, however, does touch the tarsus of a leg which must be one of the middle pair, for both fore and both hind legs can be made out separately. But the disposition of the abdomen is so obscured by the poor state of the amber in this region that it is possible for Menge to have made the above statement rather from conjecture than from actual observation, especially as he would have expected the abdomen to be longer than it actually is, believing the species to be closely related to *Apis mellifera*.

Though Menge was right in saying that the general morphology of the specimens resembles that of the honey bee in many respects, closer study has now revealed some features reminiscent of *Trigona*, such as the proportionately broad thorax, the short and round abdomen, and the small number of hamuli.

Genus *APIS* Linnaeus 1758

- *1758 *Apis* Linnaeus : 343, 575.
 1810 *Apis* Latreille : 439.
 1938 *Hauffapis* Armbruster : 43.

GENOTYPE. *Apis mellifera* Linnaeus 1758 (= *Apis mellifica* Linnaeus 1766), designated by Latreille (1810 : 439).

DIAGNOSIS. Medium-sized bees, with hair. Eyes usually hairy, clypeus not protuberant ; well-developed hind tibia, but spurs and comb lacking ; basitarsus rectangular and covered with bristles arranged in rows ; no reduction in wing venation, marginal cell always complete.

REMARKS. This genus comprises the Oligocene, Miocene and Recent Apini. They are all extremely closely related to each other, and the division into two subgenera is based on very unsatisfactory characters. Similarly, the numerous species and subspecies that have been named cannot all be maintained if the standard of Recent taxonomy is applied.

⁹ This number is incorrect of course, for Recent *Apis* workers, if it refers to the flagellar segments, since it is the drone that has twelve and the queen and worker (females) eleven segments, but it was probably computed to include the scape.

Subgenus *SYNAPIS* Cockerell 1907

*1907 *Apis* (*Synapis*) Cockerell : 229.

1931 *Synapis* Cockerell ; Statz : 42.

GENOTYPE. *Synapis henshawi* Cockerell 1907, by monotypy.

DIAGNOSIS. General morphology very much like that of Recent *Apis* but differing in the following points : labrum less tongue-shaped ; third segment of flagellum short but broad ; basitarsus, though variable in shape, never identical with Recent *Apis* ; junction of veins cu-a, Cu and the basal vein coincident, or vein cu-a lies in a slightly more proximal position.

REMARKS. This group of honey bees has been extensively treated by Statz in 1931 and 1934, who regarded it as a genus. Cockerell, however, did not grant it more than subgeneric status, regarding the venation characters as important. Cockerell's view has been adopted by the present writers.

Apis (*Synapis*) *cuenoti* Théobald 1937

*1937 *Apis cuenoti* Théobald : 401 ; pl. 8, fig. 16, pl. 28, fig. 8.

HOLOTYPE. École des Eaux et Forêts, Nancy, No. F.173 (Coll. Fliche).

DISTRIBUTION. Oligocene (Stampian), Cereste, France.

DIAGNOSIS. Length of body 13.75 mm ; eyes pubescent ; hair on body fairly plentiful ; second m-cu meets M near distal corner of cell second Rs ; forewing length 12.5 mm.

REMARKS. Not so well preserved as some other representatives of *Synapis*. Specific rank has been retained for this specimen since it is most difficult to reconcile the wealth of hair, the pubescence of the eye (compare *A. (S.) henshawi kaschkei*, p. 243, the extraordinary length of the wing and the distal juncture of second m-cu with M, with any other *Synapis*. Théobald compared it with *Apis oligocenica* (recte *A. (S.) henshawi*), and suggested some connection between the two. It is thus likely that upon re-examination the specimen may turn out to resemble this species more closely than is at present apparent.

Apis (*Synapis*) *henshawi* Cockerell 1907

*1907 *Apis* (*Synapis*) *henshawi* Cockerell : 229.

1907 *Apis* (*Synapis*) *henshawi* Cockerell ; Handlirsch : 1357.

1915 *Apis oligocenica* Meunier : 210, pl. 21, fig. 4.

1915 *Apis henshawi* Cockerell ; Buttel-Reepen : 14.

1931 *Apis* (*Synapis*) *henshawi* Cockerell ; Statz : 42.

1934 *Synapis henshawi* Cockerell ; Statz : 3, 6, tf. 1, 4, 5, 6.

1934 *Apis oligocaenica* Meunier ; Statz : 1.

1938 *Apis oligocaenica* Meunier ; Armbruster : 88.

HOLOTYPE. Museum of Comparative Zoology, Harvard University.

DISTRIBUTION. Oligocene (Aquitanian), Rott, West Germany.

DIAGNOSIS. Body 12–16 mm, forewing 8.5–10 mm. Variably hairy, eyes naked. Second m-cu meets base of cell second Rs on the abscissa of vein M beyond half-way.

DESCRIPTION. The three subspecies included in this species vary in size, the body being 12–16 mm. *A. (S.) cuenoti* would be included in this on the grounds of size, but its forewing is longer than in any known specimen of *A. (S.) henshawi*. The hairiness varies, and the hairs are perhaps sometimes plumose on the vertex. These bees closely resemble *A. mellifera* in general appearance.

REMARKS. The first description of this species is by Cockerell (1907). He examined three specimens from Rott which the Museum of Comparative Zoology, Harvard, had obtained from the firm of Dr Krantz, Bonn, under the name of *Apis dormitans* Heyden 1862. One of these specimens was named *Synapis henshawi* by Cockerell, but since the other two bore *Apis dormitans* labels, he assumed that they belonged to Heyden's species, which Cockerell regarded as different from his *S. henshawi*.

Curiously enough, Heyden also had used three specimens of the Krantz Collection for his description of *Apis dormitans*, so that it seemed possible that Heyden's specimens were those that were eventually sold to Harvard University. That this is not so, however, is revealed by the fact that Cockerell was able to describe wings of all three Harvard specimens, whilst Heyden stated that one of his specimens was 'without visible signs of wings'. Moreover, the holotype of *Apis dormitans* Heyden is in the collection of the British Museum (Natural History), and its re-examination (p. 251) has confirmed the view held by other authors that Heyden's species is not an *Apis*.

Apis dormitans Cockerell (*nec* Heyden), based on two specimens in the Harvard Collection, is a true *Apis* (*Synapis*), as was demonstrated by Statz (1931). Hence it becomes necessary to rename this form, the species name being preoccupied by Heyden's form.

Three different *Synapis* have been described from Rott. They all come from the same beds and the same biotope. In view of the variation known to exist in large *Apis* populations, they are here reduced to subspecific status.

Apis (Synapis) henshawi dormiens subsp. nov.

(Pl. 4, figs 1–5)

- *1907 *Apis dormitans* (*nec* Heyden) ; Cockerell : 228.
- 1908 *Apis dormitans* Cockerell ; Handlirsch : 1357.
- 1931 *Apis oligocenica* Meunier ; Statz : 46 (erroneously placed here).
- 1931 *Synapis dormitans* (Cockerell) ; Statz : 42, 46, figs 1a, 2b, 3c, 4a, 5–9.
- 1934 *Synapis dormitans* (Cockerell) ; Statz : 1, figs 2, 8, 10.
- 1944 *Synapis dormitans* (Cockerell) ; Statz : 63, figs 1, 3, 6.

HOLOTYPE. Museum of Comparative Zoology, Harvard University. (Cockerell's first specimen, 1907, described as *Apis dormitans*.)

PARATYPE. Second specimen ; Museum of Comparative Zoology, Harvard.

MATERIAL STUDIED. In addition to the holotype and paratype, two specimens in the British Museum (Natural History), Nos 59634 and In.36655; also all the specimens in the collection of Dr Statz, Cologne.

DISTRIBUTION. Oligocene (Aquitanian): Rott.

DIAGNOSIS. Body 13 mm, forewing 8.5 mm. Hair on vertex not plumose, eyes naked. Basitarsus with 9 rows of bristles, middle row numbering 24. Vein cu-a a little proximad of junction of basal vein with Cu.

DESCRIPTION. The medium-sized form of the species. In addition to the characters stated in the diagnosis, the following are worth noting: the flagellum is not narrowed at the base, the basitarsus is 1.6 mm long and 0.9 mm wide and the dististyle only moderately developed.

REMARKS. Numerous other specimens exist, mostly collected by Dr Statz, to whom we owe the detailed description and excellent reproduction of specimens. In 1931 Statz thought that Meunier's *Apis oligocenica* was synonymous with his *Synapis dormitans*, but after the study of Meunier's type he correctly synonymized it with *S. henschawi* (q.v.).

Apis (Synapis) henschawi henschawi Cockerell 1907

*1907 *Apis (Synapis) henschawi* Cockerell: 229.

1915 *Apis oligocenica* Meunier: 210.

1934 *Synapis henschawi* Cockerell; Statz: 5, figs 1, 4, 5, 6, 7.

1944 *Synapis henschawi* Cockerell; Statz: 63, figs 2, 5.

HOLOTYPE. Museum of Comparative Zoology, Harvard University.

OTHER MATERIAL. Holotype of *Apis oligocenica* Meunier, Heimatmuseum, Siegburg an der Lahn. Five specimens in the Statz Collection.

DISTRIBUTION. Oligocene (Aquitanian): Rott.

DIAGNOSIS. Body 15–16 mm, forewing 10 mm. Hair on vertex plumose or simple, eyes naked. Basitarsus with 10 rows of bristles (second very short), middle row numbering about 28. Vein cu-a coincident with junction of basal vein with Cu.

DESCRIPTION. This is the largest of the three subspecies. Making allowance for the distended abdomen (measured length 16.5 mm), Cockerell inferred a length of 15 or 16 mm. When Statz encountered the holotype of *Apis oligocenica* Meunier in the Siegburg Museum, he satisfied himself that it was conspecific with *A. (S.) henschawi*, and he described it in detail under that name in 1934. There appears indeed to be a close agreement between Cockerell's and Meunier's types, except that Statz states positively that the hair on the vertex is not plumose, whilst in Cockerell's specimen 'this hair appears to be plumose'. Evidently, Cockerell did not feel quite sure, and since the hair is simple in all other *Synapis*, he may have misinterpreted his specimen.

The wings are strikingly short for the size of the body. The antenna cleaner is deeply incised, semicircular, and thus differs from the shallower type present in *A. (S.) dormiens*. The basitarsus has ten rows of bristles, whilst in *A. (S.) dormiens*

only nine appear to be present, and the number of bristles comprising the middle rows is slightly larger.

Apis (Synapis) henshawi kaschkei (Statz 1931)

*1931 *Synapis kaschkei* Statz : 50, figs 10, 11.

1934 *Synapis kaschkei* Statz ; Statz : 3, figs 3, 9.

HOLOTYPE. In Statz Collection, Cologne.

DISTRIBUTION. Oligocene (Aquitanian) : Rott.

DIAGNOSIS. Body 11–12 mm, forewing 9·25 mm. Basitarsus broad, and shorter than in any known *Apis*. Vein cu-a very proximad of junction of basal vein with Cu.

DESCRIPTION. This is the smallest bee from Rott. It differs from the other two *Synapis* in the structure of the basitarsus which is very short and almost square (1·2 mm long and 1·0 mm broad). Statz, in saying that this basitarsus almost agrees with that of *Apis iridiae* Friese from Sumatra, is, however, mistaken, as this species has a pronouncedly oblong basitarsus. The depstum closely resembles that of Recent *Apis mellifera* Linn., but the wing venation places this form in the genus *Synapis*. There appear to be nine rows of bristles on the basitarsus, including the second row which is very short. It has a smaller body and a longer forewing than the other two *Synapis*.

REMARKS. Only three specimens are known, two of which, including the holotype, have been seen by one of us. Its status may have to be reconsidered when more material becomes known. For the time being, Statz's description cannot be improved upon. He figures the holotype (1931 : figs 10, 11) and a second specimen in his own collection (1934 : figs 3, 9), the latter figure being the diagram of the forewing venation derived from the two forewings of this specimen.

Subgenus *APIS* Linnaeus 1758

*1758 *Apis* Linnaeus : 343, 375.

1938 *Hauffapis* Armbruster : 43 (Genotype : *Hauffapis scheuthlei* Armbruster).

GENOTYPE. *Apis mellifera* Linnaeus 1758 (= *Apis mellifica* Linnaeus 1766), designated by Latreille (1810 : 439).

DIAGNOSIS. Third segment of flagellum shorter, but not broader, than the remaining segments ; the broadly rectangular, neatly curved basitarsus always possesses a distinct auricle ; cross vein cu-a well proximad of the junction of basal vein and Cu.

REMARKS. This subgenus contains, apart from *Apis mellifera*, with its race *A. m. indica* Fabr., the large *Apis dorsata* Fabr. of India and the small *A. florea* Fabr. of India.

The fossil forms from the Pleistocene belong to the *A. mellifera* group, and those from the Miocene also are rather closer to this Recent species than to either of the other two.

Apis (Apis) armbrusteri Zeuner 1931

1929 'Scheuthle Biene' Armbruster : 4.

1931 'Scheuthle Biene' Statz : 44, 46.

*1931 *Apis armbrusteri* Zeuner : 1292, fig. 21, pl. 8, fig. 1.

1938 *Hauffapis scheuthlei* Armbruster : 43, 92, figs 1-5, 7, 8, 14, 20, 23, 26, 29, 33, 35, 38-40, 51, 53, 55, 58, 63-65, 67, 70-72, 76, 77, 79.

HOLOTYPE. Württembergische Naturaliensammlung, Stuttgart, Boettingen Collection No. 47, individual No. 3 (head, thorax and abdomen). Cast : British Museum (Natural History) In.38859 (thorax) and In.38856 (abdomen).

PARATYPES. Württembergische Naturaliensammlung, Stuttgart, Boettingen Collection No. 47, individuals Nos 1, 2, 4-17. Casts : British Museum (Natural History) In.38857 (thorax, No. 1), In.38858 (thorax, No. 2), In.38860 (thorax, No. 4).

OTHER MATERIAL. The specimens described by Armbruster (1938) from the Upper Miocene of the Randecker Maar, all here attributed to *Apis armbrusteri* as a species. Subspecific distinctions have, however, been retained as will be seen below.

DISTRIBUTION. Upper Miocene, Württemberg.

DIAGNOSIS. A bee resembling *Apis mellifera* in size and appearance, with wax mirrors on the abdomen, the posterior edges of the sternites being apparently straight. Wings proportionately slightly broader than in the Recent species, position of the junction of the second m-cu with M, and shape of the first m-cu variable.

REMARKS. In 1931, one of us (F. E. Z.) described a fossil swarm of honey bees from the thermal limestone of Böttingen on the Swabian Alb, Württemberg, under the name *Apis armbrusteri*. It had perished in peculiar circumstances, having fallen into a fissure, on the edge of the crater of an Upper Miocene volcano, from which a spring was issuing and which released carbon dioxide into the atmosphere. Whilst these specimens afforded many details of the body structure, the wing venation could not be studied.

After the termination of the eruptions, but still in the Upper Miocene, lakes had formed in the rather larger crater of the Randecker Maar which is situated in the same volcanic area. Shales deposited in these lakes produced an abundant insect fauna, again probably because either the water or the atmosphere was temporarily poisoned. In 1926 Wilhelm Scheuthle discovered bees here.

In 1928 he was joined by Professor Armbruster, and their search resulted in the recovery of a very large number of specimens which, however, were not scientifically described until 1938, under the names of *Hauffapis scheuthlei*, *H. scheeri* and *H. scharmanni* Armbruster, with a number of subspecies. These bees provide valuable information about venation, being compressed in much the same way as the bees from Rott. The variation observed is great, but no clear line can be drawn justifying the maintenance of species. It is altogether very unlikely that in an area of 50 miles there should have existed simultaneously four hardly distinguishable species of honey bees with four more subspecies. On geographical, stratigraphical and morphological grounds, therefore, the Böttingen and Randeck bees should be regarded

as one variable species. The specific names given by Armbruster have been allotted subspecific rank, as they may be useful in the discussion of the variation, whilst Armbruster's subspecies have been synonymized with his species. In essence, this appears to represent not only ours, but Professor Armbruster's views, who in 1938 stated that he considered the Randeck bees identical with *Apis armbrusteri* Zeuner. The new names were perhaps, in part, prompted by his wish to honour some of his collaborators and colleagues.

All specimens so far recovered at Randeck and Böttingen are workers, except for a single fragment of a drone from Randeck. The following four subspecies may be distinguished.

***Apis (Apis) armbrusteri armbrusteri* Zeuner 1931**

- *1931 *Apis armbrusteri* Zeuner : 292, fig. 21, pl. 8, fig. 1.
 1934 *Apis armbrusteri* Zeuner ; Statz : 7.
 1938 *Apis armbrusteri* Zeuner ; Armbruster : 16, 45.

HOLOTYPE AND PARATYPES. See under species, above.

DISTRIBUTION. Miocene, 'Böttinger Marmor', Böttingen, Swabian Alb, Württemberg.

DIAGNOSIS. Head 2 mm, thorax 5 mm, abdomen 12 mm (distended). Mesothorax strongly vaulted, middle segment only slightly sloping. First abdominal segment very short, vertical and concave anteriorly. Posterior edges of abdominal sternites not or very little angular at mid-line.

DESCRIPTION. On a piece of red tufa measuring not more than 45 × 35 × 10 mm, 17 individuals are preserved in a layer and in a closely packed condition. The insects appear as undistorted cavities and have to be studied with the aid of casts made in an elastic material. The cavities have been broken in various positions, the abdomina (being the largest) being available most frequently. In addition, 5 thoraces and 3 heads can be studied.

Head. The eyes appear to have been oval, not kidney-shaped. They are separated on the vertex, hence the specimens may be regarded as workers.

Thorax. Almost spherical, strongly vaulted above. Prothorax short, the shoulder-buckles not reaching the tegulae. Shoulder-buckles prominent laterally in an angular fashion. Mesopleurae curved, about twice as high as long. Middle coxae long and fitted into the thorax, not pointing obliquely backwards, but vertical to the longitudinal axis of the insect. Mesonotum very strongly vaulted, more so than in *A. mellifera*, and exceeding the scutellum in height. Scutellum sharply set off and forming a prominent crosswise flange. Middle segment sloping at a smaller angle than in *A. mellifera* or even in *A. florea*.

Abdomen. Stalk short, first segment concave anteriorly, short, as seen from above. The posterior margins of the middle sternites are not angular, but more or less straight. After careful investigation, this could not be attributed to distension

or distortion of the abdomen ; it thus appears to be a sound diagnostic character. Wax mirrors present.

REMARKS. The Böttingen bees differ from the three Recent species of *Apis* in the shape of the thorax, whose mesonotum is so strongly vaulted that it exceeds the scutellum in height, a feature that may be interpreted as a sign of high specialization. Similarly, the shape of the first abdominal segment suggests specialization beyond the level of *Apis mellifera*. In other respects, however, the Böttingen bees are more primitive than *A. mellifera*, especially in the shape of the abdominal sternites, and perhaps in the slight slope of the middle segment of the thorax.

It is much to be regretted that no evidence could be obtained about the collecting apparatus or the hind legs. Attempts made to expose the legs by carefully grinding away the matrix proved unsuccessful.

A. armbrusteri was a social bee which in all probability lived much like *A. mellifera*. The wax mirrors suggest that combs were built of this substance as is characteristic of the genus *Apis*. The fact that 17 individuals were contained in a closely packed condition in the small piece of rock recovered suggests that a much larger number of bees perished and were fossilized, a swarm which would have fallen into the death trap of the Böttingen fissure and perished almost instantaneously in its poisoned atmosphere.

Apis (Apis) armbrusteri scharmanni (Armbruster 1938)

*1938 *Hauffapis scharmanni* Armbruster : 44, 113, fig. 78.

HOLOTYPE. Armbruster's specimen and fig. no. 78, in the collection of Dr Hauff, Holzmaden.

DISTRIBUTION. Upper Miocene, Randecker Maar, Württemberg.

DIAGNOSIS. Approx. 9.1 mm long ; form compact ; head massive ; abdomen plump ; corbicula (tibia) very broad but short, much reduced at base ; apex of 'pollen kneader' (counterpart of auricle, on the tibia) strong and angular ; wax mirrors elongated and hammer-shaped ; vein first R_1 possibly not arched.

DESCRIPTION. This is a small bee though the respective states of preservation have to be taken into consideration in comparing it with *A. armbrusteri armbrusteri*. The edge of the tibia, from pollen kneader to the end of the limb, forms almost a straight line, as in *A. a. scheuthlei*. Second R_s (third submarginal cell) not narrowed unduly ; second m-cu joining base of third submarginal cell more towards the middle ; cubital basis (according to Armbruster) as long as the corbicula, but reputed to be shorter than in *A. a. scheeri* ; first m-cu only a little deflected ; Cu_1 straight. The tergites of the abdomen are very narrow but very long.

REMARKS. This is in several respects a curious bee and of the several forms here discussed the one perhaps most deserving of specific rank. Unfortunately the type appears to be lost ; Armbruster had to use 'photograms' as a substitute for the specimen. Other photographs mentioned by the author appear to be of the same specimen, and no paratypes are known to exist.

Apis (Apis) armbrusteri scheeri (Armbruster 1938)

- *1938 *Hauffapis scheeri* Armbruster : 43, 92, figs 50, 52, 62, 64, 66, 69, 71, 73.
 1938 *Hauffapis scheeri* var. *gallauni* Armbruster : 45, figs 31, 59.
 1938 *Hauffapis scheeri* var. *rahdei* Armbruster : 45, fig. 50.

LECTOTYPE. Schempp Collection, Stuttgart-Weil (Armbruster 1938 : fig. 71), herein selected.

PARALECTOTYPES. Collections of Scheuthle and Schempp.

OTHER MATERIAL. Holotypes of *Hauffapis scheeri gallauni* Armbruster, No. 59 and of *Hauffapis scheeri rahdei* Armbruster, No. 50.

DISTRIBUTION. Upper Miocene, Randecker Maar, Württemberg.

DIAGNOSIS. Smaller, plumper than *A. a. scheuthlei*, with narrower third submarginal cell, and relatively short, broad and boldly formed hind tibia and basitarsus. Legs very reminiscent of those of Recent *A. mellifera*.

DESCRIPTION. Short dense hair, partly arranged in lines, occurring on the abdomen. The wax mirrors are long and narrow. The first m-cu is distinctly angular in the holotype. In most respects this form resembles *A. mellifera* greatly, and especially in the shape and size of the wing, and in certain details of the venation.

The length of the body varies ; a giant form was given the name of *H. s. gallauni* and a dwarf form *H. s. rahdei*. There is also much variation in overall size and proportions. Armbruster gave the average length of the cubital basis as 2.96 mm, though he illustrated specimens in which this measurement is 3.05, 3.2 and 3.3 mm, which thus appears to be of little taxonomic value.

REMARKS. Of this very variable subspecies, 24 specimens have been recorded. Of these, three are only doubtfully placed here. The total includes the 'giant' and 'dwarf' forms to which Armbruster gave special names.

Apis (Apis) armbrusteri scheuthlei (Armbruster 1938)

- 1929 'Scheuthle Biene' ; Armbruster : 4.
 1931 *Apis* sp. ; Zeuner : 296.
 *1938 *Hauffapis scheuthlei* Armbruster : 43, figs 63, 65, 67, 70, 72, 76, 77, 79.
 1938 *Hauffapis scheuthlei* var. *seemanni* Armbruster : 45, figs 8, 11, 21, 26, 53.
 1938 *Hauffapis scheuthlei* var. *zeuneri* Armbruster : 45, figs 36, 38.

LECTOTYPE. W. Scheuthle Collection (Armbruster 1938 : fig. 63), herein selected.

PARALECTOTYPES. Armbruster, Scheuthle, Schempp and Hauff Collections.

OTHER MATERIAL. Holotype of *Hauffapis scheuthlei seemanni* (Armbruster Coll. no. 8), and paratypes (nos 11, 21, 26, 53). Holotype of *Hauffapis scheuthlei zeuneri* (Armbruster Coll. no. 36), paratype (same collection, no. 28).

DISTRIBUTION. Upper Miocene, Randecker Maar, Württemberg.

DIAGNOSIS. Larger than *A. a. scharmanni* and *A. a. scheeri*, size slightly exceeding *A. mellifera* except in dwarf specimens. Third submarginal cell broader than in *A. a. scheeri*. Legs slender, somewhat resembling those of *A. dorsata*.

DESCRIPTION. This is the largest of the three forms of bees from Randecker Maar here recognized. Though the majority of the specimens are of the size of large Recent *A. mellifera*, giant and dwarf forms have been described. *A. s.* var. *seemanni* is a giant form, whilst the smallest specimens were named *A. s.* var. *zeuneri*. The body is covered in hair which is somewhat coarse.

Compared with *A. a. scheeri*, the legs of *A. a. scheuthlei* are longer and more slender. The hind tibia (corbicula), considered by Armbruster to be slightly curved in outline, is less narrow towards the base. The basitarsus, too, has a straighter outline. Armbruster is inclined to regard the legs as reminiscent of *A. dorsata*.

The first submarginal cell of the forewing often appears arched to meet C; the second and third submarginal cells are broader than in *A. a. scheeri*; pterostigma much reduced; the first recurrent vein is markedly angular, with a small stump of a vein at the apex of the angle.

REMARKS. Armbruster distinguished two subspecies, *A. s. seemanni* and *A. s. zeuneri*. These are here synonymized with *A. a. scheuthlei* as they are merely extreme size variants which would be found in any large population. Regarding one of the specimens assigned to *A. s. seemanni* (no. 35), Armbruster (1938: 103-4) assigned its counterpart to *A. a. scheuthlei* (no. 33) and withdrew the identification of no. 35 (1938: 114), without, however, altering the text on the earlier pages. That this should have been possible illustrates how small the difference is between these size classes.

Armbruster attached some importance to the length of the cubital basis, i.e. the base vein of cells first R₁, first Rs and second Rs. He did so presumably because it is a measure that can be taken on a comparatively large number of wings, including those the total length of which cannot be measured. In *A. a. scheuthlei* this cubital basis is reputed to equal the length of the corbicula. In fact it varies from 3.06 to 3.40 mm. In his *A. s. seemanni*, the value is 3.67 mm. Of *A. s. zeuneri* no measurements are given, except for no. 64 (Scheuthle Coll.) which is regarded as possibly referable to this form. Here it is 'apparently hardly longer than 3.0 mm'. The unreliability of this measurement has been clearly demonstrated by Alber (1949), who studied the asymmetry of the wings of bees.

Altogether 44 specimens have been assigned to this variable 'species', which Armbruster regarded as 'possibly, nay even probably' overlapping with *Apis armbrusteri* Zeuner. The wax mirrors are preserved on many of the Randecker Maar specimens, but their shape is not discussed. From the figures it appears that the margins of the sternites were more or less straight, and the wax mirrors rectangular, as in the Böttingen form.

Apis (Apis) melisuga (Handlirsch 1907)

*1907 (Apidae) *melisuga* Handlirsch: 893.

HOLOTYPE. Collection of Count Bosnianski, with counterpart; whereabouts unknown.

DISTRIBUTION. Miocene, Gabbro, Italy.

DIAGNOSIS. 18 mm long. Other features believed to be much as in *Apis mellifera*.

DESCRIPTION. Proboscis at least as long as head. Hind leg with distinct bristles along the edges. Venation not identifiable.

REMARKS. The broadened hind tibia and tarsus strongly suggest a true *Apis*. It is impossible to decide, however, how far it resembles the Recent *A. dorsata*, or differs from *A. a. scheuthlei*. It is, therefore, retained as a separate species, in the hope that fresh material will become available in the future.

Apis (Apis) mellifera Linnaeus 1758

(Pl. 4, fig. 6)

*1758 *Apis mellifera* Linnaeus : 343, 575.

1890 *Apis mellifica* Linnaeus ; Foord : 94, fig. 1.

1909c *Apis mellifera* Linnaeus ; Cockerell : 317.

SPECIMENS STUDIED. British Museum (Natural History), Palaeontology Dept., 58516, 58576.

DISTRIBUTION. Pleistocene, East African copal.

DESCRIPTION. The specimens here listed from East African copal do not differ from Recent *A. mellifera* in any essential point. Body length of specimen no. 58576 is 11 mm ; thorax 3.25 mm long and 4 mm wide ; abdomen 6 mm long and 4 mm wide. Length of wings 8.75 mm.

REMARKS. Several honey bees are known from the copal of East Africa. Foord (1890) mentioned two specimens side by side. His poor figure suggests the shape of the basitarsus being identical with *A. mellifera*.

Cockerell (1909c) examined two specimens from the Cambridge Collection. They were at first believed to be enclosed in Yarmouth amber and hence to be of Eocene age, but he considered it much more likely that sailors had brought them from East Africa for the Yarmouth trade in amber fossils.

Specimen no. 58576 has been studied in detail. Its wing venation is remarkable in two respects ; the first submarginal cross vein (first abscissa of Rs) is S-shaped, and vein first m-cu (first recurrent) appears to lack the usual angularity. The peculiar shape of the submarginal cross vein is known also in *Synapis*, as well as in *A. florea* and to a lesser extent in *A. dorsata*. One might, therefore, regard it as a primitive character, but since it occurs also in a specimen of *A. mellifera* from Entebbe, Uganda, it appears to have persisted in some East African bees. The lack of angularity of first m-cu is believed to be a mere accident of preservation ; angularity indeed probably does exist, though it may not be very marked, and it is masked in this specimen by a slight fold in the wing.

The abdomen of the East African copal bee has yellow bands, like its modern counterpart.

Family APIDAE *incertae sedis*
'*Apis*' *aquitaniensis* de Rilly 1930

- *1930 *Apis aquitaniensis* de Rilly (not seen).
1931 Abeille mellifère ; Alphanbéry : 3, fig. on p. 3.
1938 *Apis aquitaniensis* de Rilly ; Armbruster : 88.
1950 *Apis aquitaniensis* de Rilly ; de Rilly : 45.

HOLOTYPE. Muséum Marseille, No. 5979, as stated by both Armbruster (1938) and Roussy (personal communication). Repeated enquiries, however, have not succeeded in eliciting its present whereabouts.

DISTRIBUTION. Oligocene (Aquitanian) : Aix-en-Provence.

DIAGNOSIS. Length of body 16 mm, length of thorax 5 mm, length of abdomen 9 mm, length of forewing 10 mm, length of hind leg 7.5 mm.

DESCRIPTION. According to Alphanbéry, two antenna are visible on the head, and one eye is well preserved. The rest of the head is badly crushed but its general shape is triangular, like heads of bees with mandibles in general. The thorax is also crushed and has a black depression in the centre. On its edges there are two orange-coloured ridges. The left wing is beautifully spread and shows all the characteristics of a honey bee. The third pair of legs is well spread out, and the tibia shows a broadening suggestive of a pollen basket. Five abdominal segments can be distinguished.

This description is an almost literal translation from Alphanbéry (1931).

REMARKS. This specimen was first mentioned in an article by F. de Rilly (1930) entitled *L'abeille fossile française*, of which nothing further is known. It may be identical with an article said to have been written by that author in 1924, which we have not seen either. Alphanbéry's description is vague. His reference to the left wing showing 'all the characteristics of the honey bee' is perplexing when applied to an Oligocene species, and his figure is useless. Armbruster, aware of this, was fortunate enough to receive a facsimile in coloured plastic from F. de Rilly. This, however, was scarcely the likeness of an *Apis*.

Through the kindness of Monsieur Roussy we have been able to inspect a similar facsimile and we agree with Armbruster's conclusion. But the question arises as to whether the fault lies with the facsimile.

A paper by de Rilly (1950) appears to answer this question. In it he asserts once again his claim that the specimen under discussion is an *Apis*, but with 'quelques caractères archaïques (cellule supplémentaire de l'aile, éperon tibial)'. According to an enlargement of the wing (published in 1924) and reproduced in facsimile, however, the supplementary cell is that formed by a cross vein to the marginal cell, which is thus a cell completely unknown in Apidae. Moreover, the pterostigma is exceptionally large and deep. The éperon-tibial, which undoubtedly belongs to the hind tibia (since the tibial spur of the middle leg, being always present in *Apis*, affords no diagnostic character) is worth something, in that it rules out the genus *Apis* proper. The few positive indications which have been made available in de

Rilly's work (1950) prove that this specimen is not an *Apis*, and probably not even a member of the Apidae.

'Apis' dormitans Heyden 1862

- *1862 *Apis dormitans* Heyden : 76, pl. 10, fig. 8.
 1891 *Apis dormitans* Heyden ; Scudder : 689 (5927).
 1907 *Apis dormitans* Heyden ; Cockerell : 228.
 1907 *Apis dormitans* Heyden ; Handlirsch : 892.
 1908 *Apis dormitans* Heyden ; Handlirsch : 1357.
 1915 *Apis* (?) *dormitans* Heyden ; Buttel-Reepen : 13.
 1915 *Osmia dormitans* (Heyden) ; Buttel-Reepen : 14.
 1915 *Apis dormitans* Heyden ; Meunier : 210.
 1931 *Osmia dormitans* (Heyden) ; Statz : 42.
 1931 *Apis dormitans* Heyden ; Statz : 42.

HOLOTYPE. British Museum (Natural History), 58778.

DISTRIBUTION. Oligocene (Aquitanian) : Rott am Siebengebirge.

REMARKS. According to Carl von Heyden three specimens existed but the first was very poorly preserved and he was far from happy about placing it in the genus *Apis*. The second and third specimens were too meagrely described for recognition. Buttel-Reepen considered that the whole habitus, the rounding off of the abdomen and the great breadth of the thorax compared with the breadth of the head, indicated, not an *Apis*, but an *Osmia*. Meunier considered it to be some kind of worker bee, but referred to it as a very enigmatical form. All authors agree that it has not been proved to be an *Apis*.

The re-examination of the holotype, which was damaged by water during the war, confirms the views of previous authors. No character is preserved which would justify placing it in *Apis*, and the rounded end of the abdomen precludes it from being included in this genus. The venation, which Heyden also shows in his figure, is too poor for generic identification.

Two further specimens of '*A. dormitans*', from Rott, now in the Museum of Comparative Zoology, Harvard University, were investigated by Cockerell (1907). They are specifically different from the specimens referred to above but are legitimate members of *Apis* (*Synapis*). Hence they require a new name, and have been described as *Apis* (*Synapis*) *henshawi dormiens* n. subsp. (p. 241).

'Apis' styriaca Pongrácz 1931

- *1931 *Apis styriaca* Pongrácz : 105.
 1938 *Apis styriaca* Pongrácz ; Armbruster : 88.

HOLOTYPE. Whereabouts not known.

DISTRIBUTION. Miocene : Parschlug.

REMARKS. A wing fragment only has been referred to, but not described. Its affinities are wholly obscure, and the name must be treated as a *nomen nudum*.

'Bombus' carbonarius Menge 1856

- 1856 *Bombus* Latreille ; Menge : 26.
 *1856 *Bombus carbonarius* Menge : 27.
 1886 *Bombus* Latreille ; Brischke : 278.
 1891 *Bombus carbonarius* Menge ; Scudder : 690 (5950).
 1907 *Bombus carbonarius* Menge ; Handlirsch : 891.
 1909d *Bombus carbonarius* Menge ; Cockerell : 5.
 1928 *Bombus carbonarius* Menge ; Wheeler : 97.
 1931 *Bombus carbonarius* Menge ; Salt : 143.

DISTRIBUTION. Eocene : Baltic amber.

REMARKS. Apparently Menge had five specimens in two blocks of amber, but only two species were present, which he called *B. carbonarius* and *B. pusillus*. No diagnosis or description was ever published.

'Bombus' muscorum Roussy 1937

- non 1935a *Bombus muscorum* (Linnaeus) ; Richards : 73.
 *1937 *Bombus muscorum* Roussy : 58.

DISTRIBUTION. Eocene : Baltic amber.

HOLOTYPE. Whereabouts unknown.

DESCRIPTION. A solitary bee, red and black, and abundantly hairy. No further details.

REMARKS. Cannot be assigned to any genus on the characters given.

'Bombus' pusillus Menge 1856

- 1856 *Bombus* Latreille ; Menge : 26.
 *1856 *Bombus pusillus* Menge : 27.
 1891 *Bombus pusillus* Menge ; Scudder : 691 (5954).
 1907 *Bombus pusillus* Menge ; Handlirsch : 891.
 1909d *Bombus pusillus* Menge ; Cockerell : 5.
 1928 *Bombus pusillus* Menge ; Wheeler : 96.

DISTRIBUTION. Eocene : Baltic amber.

REMARKS. See '*Bombus' carbonarius* Menge above.

'Bombus' antiquus Heyden 1859

- *1859 *Bombus antiquus* Heyden : 12, pl. 2, fig. 4.
 1862 *Bombus antiquus* Heyden ; Heyden : 75.
 1891 *Bombus antiquus* Heyden ; Scudder : 690, pl. 31, fig. 4 (5949).
 1907 *Bombus antiquus* Heyden ; Handlirsch : 891.
 1931 *Bombus antiquus* Heyden ; Cockerell : 309.
 1936 *Bombus antiquus* Heyden ; Statz : 260.

HOLOTYPE. Whereabouts now unknown. Originally in von Dechen's collection.

DISTRIBUTION. Oligocene (Aquitanian) : Rott am Siebengebirge.

REMARKS. Specimen lacking several parts and even Heyden (1862) considered it 'perhaps not different from *Osmia carbonum*', thus making its generic status very insecure. There is no useful purpose served in synonymizing it with the latter species, since Heyden's statement is far too casual, and possibly had little real significance. No subsequent author has considered the specimen to be 'good'.

'*Bombus*' *grandaevus* Heer 1849

- *1849 *Bombus grandaevus* Heer : 96, pl. 7, figs 3a, b.
- 1856 *Bombus grandaevus* Heer ; Giebel : 182-183.
- 1867 *Bombus grandaevus* Heer ; Heer : 5, pl. 3, figs 6, 7.
- 1891 *Bombus grandaevus* Heer ; Scudder : 690 (5952).
- 1895 *Bombus grandaevus* Heer ; Scudder : 122.
- 1907 *Bombus grandaevus* Heer ; Handlirsch : 891.
- 1928 *Bombus grandaevus* Heer ; Wheeler : 97.
- 1931 *Bombus grandaevus* Heer ; Cockerell : 309.
- 1938 *Bombus grandaevus* Heer ; Armbruster : 87.

HOLOTYPE. Badische Landessammlung für Naturkunde, Karlsruhe. Not traced. (Heer 1849 : fig. 3.)

ANOTHER SPECIMEN. As figured by Heer (1867).

DISTRIBUTION. Miocene : Radoboj.

REMARKS. Cockerell regarded this form as generically unclassifiable. Scudder thought it was not a *Bombus*, but possibly belonging to *Eucera*. Handlirsch (1907) also believed that it belonged near *Eucera* but to a new genus. Heer's illustrations provide no help. They suggest, however, that two different specimens were in existence, those figured in 1849 and 1867.

We have made enquiries at Karlsruhe and visited the Museum, but the specimens cannot be found. It is possible they may come to light when the material packed away in the cellars during the war is sorted out.

'*Bombusoides*' *mengei* Motschulsky 1856

- *1856 *Bombusoides Mengei* Motschulsky : 28.
- 1891 *Bombusoides mengei* Motschulsky ; Scudder : 691 (5955).
- 1907 *Bombusoides mengei* Motschulsky ; Handlirsch : 892.
- 1909d *Bombusoides mengei* Motschulsky ; Cockerell : 5.
- 1928 *Bombusoides mengei* Motschulsky ; Wheeler : 97.

DISTRIBUTION. Eocene : Baltic amber.

DESCRIPTION. A bumble bee not more than $1\frac{1}{2}$ lines (3.175 mm) long. No further description provided.

REMARKS. On formal grounds this is the genotype of *Bombusoides* Motschulsky. The holotype is lost. The size given is much too small for any bumble bee.

Apidae gen. et sp. indet. 1 (Brischke)

- 1886 *Bombus* Latreille ; Brischke : 278.
 1891 *Bombus* Latreille ; Scudder : 690 (5946).
 1907 *Bombus* Latreille ; Handlirsch : 891.

DISTRIBUTION. Eocene : Baltic amber.

REMARKS. A single '*Bombus*' mentioned but not described. Probably either *B. carbonarius* Menge or *B. pusillus* Menge, both *nomina nuda* (p. 252).

Apidae gen. et sp. indet. 2 (Brischke)

- 1886 *Melipona* Brischke : 278.
 1891 *Melipona* (vic.) Brischke ; Scudder : 716 (6175).
 1896 *Melipona* Tosi : 356.
 1907 *Melipona* (vic.) Brischke ; Handlirsch : 892.

DISTRIBUTION. Eocene : Baltic amber.

DESCRIPTION. 'Venation is reminiscent of the South American genus *Melipona* but differs in the structure of the legs.'

REMARKS. Two specimens appear to have been known to Brischke, but the described specimens are now lost. The comparison with *Melipona* means little in view of the existence of the meliponoid *Electrapis*.

Apidae gen. et spec. indet. 3 (Burmeister)

- 1832 *Trigona* Burmeister : 636.
 1836 *Trigona* Burmeister : 577.
 1856 *Trigona* Burmeister ; Giebel : 184.
 1891 *Trigona* (?) Burmeister ; Scudder : 733 (6324).
 1896 *Trigona* Tosi : 356.
 1907 *Trigona* (?) Burmeister ; Handlirsch : 892.

DISTRIBUTION. Eocene : Baltic amber.

REMARKS. Perhaps identical with *Electrapis* (*Roussyana*) *palmnickenensis* (p. 233). Specimen lost.

Apidae gen. et sp. indet. 4 (Scudder)

- 1881 *Bombus* Scudder : 290.
 1883 *Bombus* Scudder : 280.
 1891 *Bombus* Scudder : 690 (6947).
 1907 *Bombus* Scudder ; Handlirsch : 891.

DISTRIBUTION. Oligocene : Florissant.

REMARKS. One of the specimens of bees which Scudder knew from Florissant was assigned to *Bombus* without further description or comment.

NOT APIDAE

Lithoblatta lithophila (Germar 1839)

- *1839 *Musca lithophila* Germar : 222.
 1864 *Blattidium beroldingianum* Heer : 300, fig. 8.
 1869 *Musca lithophila* Germar ; Weyenbergh : 256, pl. 34, fig. 2 (no. 6511).
 1869 *Bombus* (?) *conservatus* Weyenbergh ; Weyenbergh : 259, pl. 34, fig. 7.
 1869 *Apiaria veterana* Weyenbergh ; Weyenbergh : 260, pl. 34, fig. 8 (no. 6480 *nec* 6431).
 1886 *Mesoblattina lithophila* (Germar) ; Scudder : 464.
 1886 *Mesoblattina lithophila* (Germar) ; Deichmüller : 6, pl. i, figs 1-6.
 1888 *Mesoblattina lithophila* (Germar) ; Oppenheim : 221, pl. 30, figs 6, 8.
 1895 *Mesoblattina lithophila* (Germar) ; Meunier : 223.
 1898 *Mesoblattina lithophila* (Germar) ; Meunier : pl. 25, figs 76-78 ; pl. 26, figs 85-86 ; pl. 27, figs 92-93.
 1898 *Naucoris carinata* Meunier : pl. 27, fig. 88.
 1907 *Lithoblatta lithophila* (Germar) ; Handlirsch : 530, pl. 46, fig. 7.
 1931 *Bombus conservatus* (Weyenbergh) ; Cockerell : 309.

HOLOTYPE. Whereabouts not known, probably lost.

SPECIMENS STUDIED. Teyler Museum, Haarlem, Netherlands, No. 15324 (*Bombus conservatus*) and No. 15305 (*Apiaria veterana*).

DISTRIBUTION. Upper Jurassic : Solnhofen, Bavaria.

REMARKS. Meunier regarded both *B. conservatus* and *A. veterana* as cockroaches (*Mesoblattina*). His view was shared by Handlirsch who identified them with Germar's *Musca lithophila* and erected the new genus *Lithoblatta*. Thus the supposed bees of the Upper Jurassic have proved to be Orthoptera.

The specimens in Haarlem which we have studied support this view. No. 15324 has an orthopteroid habitus, and No. 15305 has long antennae and orthopteroid tibia. Cockerell, who saw *B. conservatus*, also held that it is 'wholly obscure and there is no reason for regarding it as a bee'.

VI. APPENDIX

by S. F. Morris

Colletidae gen. et sp. indet.

1927 *Colletidae* ; Blair : 139.

MATERIAL. Whereabouts unknown.

DISTRIBUTION. According to Blair the material is 'perhaps Upper Pliocene, perhaps Quaternary or probably Sub-recent'. Oil sands ; near Fyzabad, Trinidad.

Ctenoplectrella splendens Kelner-Pillault 1970

*1970a *Ctenoplectrella splendens* Kelner-Pillault : 13, pl. 1, figs 3, 4.

MATERIAL. Holotype : Geologisch-palaeontologischen Institut der Universität, Göttingen. Paratype : No. 49, Zoologisches Museum der Humboldt-Universität, Berlin.

DISTRIBUTION. Eocene, Baltic amber.

Anthidiini gen. et sp. indet.

1972 *Anthidiini*; Sando: 424.

MATERIAL. Gerard Germs Collection.

DISTRIBUTION. Recent (collected from rocks of Precambrian and Lower Palaeozoic age).

Osmia sp.

1972 *Osmia* sp.; Sando: 421.

MATERIAL. United States National Museum; United States Geological Survey, Glacier National Park Museum; Harvard University, Paleobotany Collection.

DISTRIBUTION. Recent (in rocks of Precambrian to Upper Palaeozoic age), Montana, Wyoming.

***Apoidea* (? *Anthophorinae*)** sp.

1969 *Apoidea* (? *Anthophorinae*) sp.; Werner: 12, pl. 19, fig. 3.

MATERIAL. United States National Museum 257, B.218.

DISTRIBUTION. Early Pleistocene, Rita Blanca lake deposits.

Probombus hirsutus Piton (ms)

1940 *Probombus hirsutus* Piton (ms): 218.

1969b *Probombus hirsutus* Piton; Kelner-Pillault: 526 (*nomen nudum*).

DISTRIBUTION. Eocene, Menat, Puy-de-Dôme, France.

Trigona (Hypotrigona) eocenica Kelner-Pillault 1970

*1970b *Trigona (Hypotrigona) eocenica* Kelner-Pillault: 437, figs 1-3.

MATERIAL. Holotype: Geologisch-palaeontologischen Institut der Universität, Göttingen. Paratype formerly in the Geological Museum of the University, Königsburg; now in the Humboldt Museum, Berlin.

DISTRIBUTION. Eocene, Baltic amber.

Trigona (Hypotrigona) dominicana Wille & Chandler 1964

*1964 *Trigona (Liotrigona) dominicana* Wille & Chandler: 188, figs 1-5.

MATERIAL. Holotype and five paratypes in the collection of the Illinois Natural History Survey.

DISTRIBUTION. Oligocene, Dominican Republic.

***Trigona (Nogueirapis) silacea* Wille 1959**

*1959 *Trigona (Nogueirapis) silacea* Wille : 849, pl. 119, text-figs 1-4.

1964 *Trigona (Nogueirapis) silacea* Wille ; Wille : 120, fig. 1.

MATERIAL. Holotype : 12601. Paratypes : 12602-11. In University of California Museum.

DISTRIBUTION. Middle Miocene, Simjovel, Chiapas Province, Mexico.

***Electrapis minuta* Kelner-Pillault 1970**

*1970a *Electrapis minuta* Kelner-Pillault : 16, pl. 2, figs 3, 5B.

MATERIAL. Syntypes : Geologisch-palaeontologischen Institut der Universität, Göttingen ; Block 50a, Zoologisches Museum der Humboldt-Universität, Berlin.

DISTRIBUTION. Eocene, Baltic amber.

***Apis catanensis* Roussy 1960**

*1960 *Apis catanensis avolii* Roussy : 8, fig. 2.

1969b *Apis catanensis avolii* Roussy ; Kelner-Pillault : 524.

MATERIAL. One specimen in the private collection of Anastasi and Guiseppe Avolio, jewellers of Sicily.

DISTRIBUTION. Miocene, near Catania, Sicily.

REMARKS. Roussy used the trinomen *Apis catanensis avolii*, but since the species was not split the third name is superfluous.

? Apoidea sp.

1821 Vast numbers of bees and nests ; Henslow : 501.

MATERIAL. Whereabouts unknown.

DISTRIBUTION. Parish of Kirk Balaft, Isle of Man ; ? Pleistocene.

Not Apoidea

1962 Native bee ; Carroll : 264, fig. 1.

MATERIAL. Melbourne University, Geological Dept., M.U.G.D. 3518.

DISTRIBUTION. ? Lower Jurassic, Koonwarra, South Gippsland, Victoria, Australia.

VII. ACKNOWLEDGEMENTS

The task of an amanuensis is a difficult one, but to undertake the publication of a manuscript on a subject with which one is unfamiliar, and whose authors one did not work with or even know, requires a particular courage and dedication. Thus,

great credit is due to Mr S. F. Morris for his initiative in revivifying the manuscript and in undertaking much of the editorial work towards its publication. Thanks are also due to Mr D. L. F. Sealy who prepared the paper for the press, and to Professor O. W. Richards for his advice.

H. W. BALL
Keeper of Palaeontology

VIII. REFERENCES

[Although every effort has been made to trace all the references cited in the text, in a few cases, indicated below by *, this has unfortunately not been possible; though bibliographic references can be given in most instances, they must be cited as 'not seen' (by the Editor). It is evident that some works which were available to the authors are not now to be obtained in any British library. The Editor gratefully acknowledges the assistance of the librarians of the British Museum (Natural History) in his efforts to trace the missing works. Though not cited in the text, references marked † are known to have been consulted by the authors during the preparation of this paper. They are included as a contribution to the general bibliography of the subject. S. F. M.]

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